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Rhode Island University

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VOL. 1 OF 2

ENVIRONMENTAL RELATIONSHIPS OF BENTHOS IN SALT PONDS

TECHNICAL REPORT NO. 3

January 1, 1960 - December 31, 1964

Approved for distribution

Charles J. Fish
Principal Investigator

John A. Knauss
Dean

Public Health Service
Grant No. WP-00023

FORWARD TO TECHNICAL REPORT NO. 3

The terminal technical report No. 3 which follows is mostly concerned with plant relationships and the physical and chemical environment. In the original proposal of the Salt Pond Project, ENVIRONMENTAL RELATIONSHIPS OF BENTHOS IN SALT PONDS, WP-00023, page 4, paragraph A-2 stated that the specific aims of this program were as follows: "To determine (a) seasonal changes in amounts and distribution of fixed macroscopic vegetation, as related to sediment type and water movement; (b) production rates of fixed vegetation and of phytoplankton and contribution of each to the total pond productivity; (c) whether the fixed vegetation derives most of its nutrients from the soil or, in competition with the phytoplankton, from the water; and (d) the contribution of the rotting fixed vegetation (after it has been torn loose) to the nutrition of the phytoplankton." Also, specific aims were set out in paragraph A-3 for the analysis of the physical environment. This technical report includes studies, experiments and survey data which largely answer all of these aims in detail. Two of the papers included in this report, 5-1 and 6-1 et seq., are preprints of work in press. The rest of the report includes papers complete or nearly complete for publication. Other papers are in preparation using much of the data from this study.

This report has been separated into two bound volumes for purposes of convenience. Since many of the maps and graphs are used concurrently with various sections of the text, separation of the data from the text makes it possible for the reader to view text and data simultaneously. This approach was used to heighten the usefulness of the graphical analysis method employed. Statistical treatment of these data are now in progress with Dr. Sanders Bolton, but the significance of various events and correlations are so graphically convincing, a simple treatment devoid of sophisticated mathematics was considered more appropriate. All figures enumerated with an "A-", e.g., A-1, A-2, etc., will be found in the appendix volume. All other figures are text figures.

A general bibliography is provided at the close of the text volume for all sections which are not preprint material. It is to be understood that the bibliography is not complete. No exhaustive search and citation of the literature was attempted. Only the most pertinent papers are listed.

Workers using ideas and data given in this report should refer to this publication as a technical report furnished to the National Institute of Health, cite: Tech. Rpt. III, WP-00023, NIH, Grad. Sch. of Oceanography, Univ. of R. I., Kingston, R. I., Jan. 1966.

ACKNOWLEDGEMENTS

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Stimulus and guidance for the broad outlines of this study were provided by Dr. Charles J. Fish, senior investigator on the Salt Pond Project begun in January of 1960. The writer is grateful for some stimulating discussions regarding the study with Mr. Theodore J. Smayda, Dr. Robert L. McMaster, Dr. Richard D. Wood, Dr. Robert J. Conover, Dr. John Zeigler, Dr. Howard Sanders, and Mr. Charles Yentch. Grateful acknowledgement is especially given to Dr. John McN. Sieburth, of this laboratory, whose critical views and counsel have been a constant source of stimulation and inspiration. Acknowledgement is given to the maintenance staff, office staff, and the administration of the Graduate School of Oceanography and the University for helping make this research program possible.

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GENERAL INTRODUCTION

The present volume contains the terminal series of reports on environmental relationships of benthos in coastal salt ponds based on studies conducted in Charlestown and Green Hill Ponds during the period January 1, 1960 to December 31, 1964. The first, a progress report on investigations during the year 1960 under the current Public Health Service Grant, was distributed in January 1961. A second, designated Technical Report No.2, covering the period January 1, 1962 to October 1, 1964, represented a final report on one of the major projects, that of Harry P. Jeffries, William P. Dillon and associates on benthic animal and physical environmental relationships, dated 15 October 1964. A general resumé of the program, a series of papers on benthic plant relationships, and auxiliary reports, including a geological study, comprise the present volume, Technical Report No.3.

Published and unpublished reports on studies conducted under the present contract are listed on page 1-11. Several additional papers on pelagic plant productivity and relationships are being prepared by T. J. Smayda and assistants for inclusion as a technical report in this series. The program as outlined in 1960 (page 6) and 1961 will then be considered to have been completed except for the macro-epibenthic invertebrates. This important component of the population could not be adequately analyzed and evaluated because of the unavailability of qualified personnel. It is believed, however, that the Systematic-Ecology Program of investigations of estuarine benthos in the neighboring Woods Hole region by H. R. Carriker and associates will produce much data applicable to comparable biota in Charlestown and Green Hill Ponds. As a substitute for the macro-epibenthic study, other areas of research were expanded.

Previous Investigations. Preliminary studies in Charlestown and Green Hill Ponds were first initiated by Narragansett Marine Laboratory personnel in 1927 as part of a program of research on the importance, conservation and exploitation of Rhode Island's marine resources (Fish, 1955).

It has long been known that there is considerable variation in the natural populations of animals and plants in the saline ponds bordering the Rhode Island shoreline due to differences in size, depth, salinity, character and amount of land drainage, breachways, and biological productivity. In addition to their recreational and economic value as readily accessible sources of shellfish, blue crabs (*Callinectes sapidus*, Rathbun), fin fish and aquatic game birds, their importance in augmenting the rich natural resources of the outer bay and adjacent coastal waters is also generally recognized. For sound conservation, each body of water would need to be individually appraised, its potentialities ascertained and decisions made on the role it should play in the State's economy. This involves a determination of the kind of marine crops which the area is best fitted to produce or can be made to produce and, where feasible, breachway construction to provide the particular salinity and circulation control necessary for support of the desired species. In several instances, lucrative oyster and other shellfisheries have been destroyed or adversely affected by channel enlargement and resultant salinity increase. Conversely, permanent breachway construction permits the necessary free entrance and exit for a most important endemic fin fish, the winter flounder (*Pseudopleuronectes americanus*, Walbaum), other food fish species including smelt (*Osmerus mordax*, Mitchill), white perch (*Morone americana*, Gmelin) and alewives (*Pomolobus pseudoharengus*, Wilson) and a summer recreational attraction, the blue crab. It also insures important refuge nurseries for the young of some of the more important endemic and migratory food fishes such as the tautog (*Tautoga onitis*, Linnaeus), blue fish (*Pomatomus saltatrix*, Linnaeus), scup (*Stenotomus versicolor*, Mitchill) and butterfish (*Poronotus tricanthus*, Peck) until old enough to fend for themselves.

During the period 1937 to 1942, Marie P. Fish included these ponds in a general investigation of production, growth and dispersal of marine fishes in Narragansett Bay and its tributary waters. Her investigation provided a basis for evaluating the relative importance of the ponds as fin fish production areas and also revealed their value as refuge nurseries for appreciable numbers of both endemic bay residents and the important above mentioned migrants during their critical first summer growth period. A manuscript and all data on these studies were lost in a fire which destroyed the Laboratory in 1959.

During this period various other special studies of a survey nature were conducted in Charlestown and Green Hill Ponds by different individuals, including Hicks on physical hydrography, Hard on sedimentation, Wright, Cheadle and Palmatier (1949) and Wood and Palmatier (1954) on attached vegetation, and Jeffries on zooplankton. While much valuable information was gained in these more or less independent investigations, it was clear that for a solution of major resource problems involving natural productivity in any estuarine waters it would be necessary to understand the interaction of both the environmental variables and the biological processes which ultimately control production of the biota and are prerequisite to any sound program of resource management. It was also evident that for a proper understanding it would be necessary to conduct the studies in areas as yet unaffected by industrial and domestic pollution. Charlestown and Green Hill Ponds, conforming to this requirement and differing in their rates of biological production, were selected for an integrated study when investigations were resumed in March 1954 by T. E. Bowman and continued by R. J. Conover from August 1955 to February 1958 (Conover, 1959, 1961). Observations of temperature, salinity, oxygen, inorganic phosphate and nitrate, chlorophyll _a_, and zooplankton displacement volumes were made periodically.

Conover found that there is some salinity stratification and a two-layered transport system through the single breachway, with phosphate derived principally in influx from offshore waters. The breachway is thus not only of great importance for access and exit of biota, but also for the greater productivity observed in its proximity contrasted with more distant parts of the pond. The influence of the exchange in these brackish embayments where the major marine stocks feed principally on phytoplankton was considered with regard to the effect of a depletion of the phytoplankton crop on the growth rates of the local shellfish stocks.

The existing status of the pond system and possible alterations which might be affected to further control production of marine crops were also discussed by Conover (1959, 1961). He emphasized the importance of dilution from land outwash in creating water of different densities and a resulting two-layered system with less dense water flowing out at the surface and dense water from offshore entering along the bottom. According to Conover, "The interaction of the two components moving in opposite directions creates an 'eddy' which can concentrate nutrients and organisms." The sill in ponds of this sort forms, he found, a natural "culture basin" provided with both a frequently renewed culture medium and an entrapment mechanism to prevent excessive loss of the products of the culturing process. He further pointed out the danger as well as the advantages in altering a natural breachway and the careful study which should precede such action. In this regard, he reviewed the recent history of the ponds and cited evidence that a critical exchange rate had already been exceeded in Charlestown Pond, presumably through dredging operations in 1952 and 1956. It was Conover's opinion that most primary production in the ponds would be found to be associated with the dense growth of attached vegetation, spermatophytes and algae.

As in earlier programs in other areas, Lake Erie (Fish, _et al_, 1960) and the Bay of Fundy (Fish and Johnson, 1937; Fish, 1955; Gran and Braarud, 1935; and Watson, 1936), where basic research was found an essential preliminary in the solution of major applied biological resource problems, it was recognized that a more comprehensive program of correlated basic research would be necessary for an understanding of estuarine biological oceanography and to establish the validity of the various practical hypotheses which had been offered on salt pond resource management.

At the inception of the present program, Charlestown Pond was recognized as an unusually productive lagoon. With the conclusion of these studies it has become even more apparent that this body of water is a "standard of comparison" for less productive tidal ponds in cool temperate climates. The data from which the bioproduction, nutrient and carbon cycles have been interpreted may be used in the future to represent the consequences of a model estuarine ecosystem.

ENVIRONMENTAL RELATIONSHIPS OF BENTHOS IN SALT PONDS

The specific research plan, approved by the Public Health Service and initiated on 1 January 1960 involved the following objectives grouped in three general categories:

1. Benthic Animal Relationships. (a) To analyze qualitatively and quantitatively the fauna (and flora) and to evaluate the relative importance of the component species; (b) to identify the principal environmental factors influencing the abundance and distribution of both the "infauna" (animals living in the sediment) and the "epifauna" (animals living on the bottom surface); and (c) to evaluate seasonal changes in B.O.D. and hydrogen sulfide produced under natural conditions, and their influence on the animal (and plant) populations.

2. Plant Relationships. To determine (a) seasonal changes in amounts and distribution of fixed macroscopic vegetation, as related to sediment type and water movement; (b) production rates of fixed vegetation and of phytoplankton, and contribution of each to the total pond productivity; (c) whether the fixed vegetation derives most of its nutrition from the soil or, in competition with the phytoplankton, from the water; and (d) the contribution of the rotting fixed vegetation (after it has been torn loose) to the nutrition of the phytobenthon, phytoplankton, and ultimately the dependent faunal communities.

3. Physical Environmental Interrelations. The continued existence of both animal and plant benthic communities results from the interaction of the water mass and bottom which affects (a) the influx of nutrients and recruitment of pelagic stages; (b) establishment and maintenance of the resultant benthic communities; and (c) dispersal of pelagic stages. These factors in turn must be evaluated in terms of (a) fresh-water introduction, (b) turbulence and circulation patterns within the ponds, and (c) interchange with open coastal waters. To these ends

the following specific aims are considered essential: (a) to determine the processes involved in bringing about the existing rates of exchange of fresh and salt water throughout the estuary by evaluation of the following three factors and their composite action: (1) tide and tidal current relationships, (2) quantity and fluctuations of fresh-water inflow, and (3) evaluation of wind and tide induced circulation; (b) to measure current velocity profiles as a function of nutrient exchange, bottom type and vegetation since plants form obstacles in the current flow pattern distorting normal erosion and sediment deposition, and as a function of bottom plant metabolism; (c) to measure wind induced turbulence as it affects horizontal and vertical movements of nutrients, bottom sediments and benthos; (d) to evaluate the relative importance of the non-tidal currents as they influence dispersal and interchange with open coastal waters; (e) to study the influence of environmental factors in determining the seasonal cycle of change in the states of sediment penetrability of compaction; and (f) as an additional objective envisioned from the beginning of the program, to consider the deposition and entrainment of organic carbon and its implications in the pond's present and past history.

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THE PHYSICAL AND GEOLOGICAL OCEANOLOGY OF CHARLESTOWN AND GREEN HILL PONDS, R. I.

by

J. T. Conover and Wm. P. Dillon

Introduction

The physical, geological, and chemical oceanology of Charlestown and Green Hill Ponds was described by R. J. Conover (1961). His survey was made eight years ago. A second survey of the same lagoon, reported in this series, was conducted from 1960 through 1964. The two surveys provide a unique opportunity for comparisons and a reevaluation of the processes taking place in an estuary.

In the following account, the physical environment is analyzed in terms of substrates (bottom) and the carrier (water column) as related to living communities. There is some deliberate repetition of material from Volume II, of this series, in those instances where these data and concepts are pertinent to the discussion. The intention here is to integrate the living and non-living systems in search of the causal principles which are responsible for the specific consequences of seasonal and superannual or constant events in the lagoon.

The Sedimentary Environment

Along the southern shores of New England there are a series of coastal lagoons extending from the western part of Connecticut eastward to Chatham, Cape Cod, Massachusetts. The majority of these lagoons have a common origin as shallow, stream-cut outwash valleys left in the wake of the retreating Wisconsin glacier 11,000 years ago. Most of these lagoons have an average depth of one to two meters. Many of the lagoons are partially or entirely closed by barrier beach bars. Some lagoons have a considerable amount of fresh-water entering the system keeping a singular breachway open, while embayments have varying amounts to relatively little inflowing fresh-water, and as a consequence have undergone more rapid change leading toward a marshland, sand dunes, or uplands with a complete disappearance of the estuary.

Charlestown and Green Hill Ponds represent one of the more typical late or terminal stage types of coastal lagoons. The lagoon surveyed is located (71°39'W.Long. 41°22'N.Lat.) in the southern part of Washington County, Rhode Island, about seven miles west of Point Judith. Charlestown Pond lies parallel to the coast, is almost four miles in length and from less than a quarter of a mile to half a mile in width (Figure A-1). Charlestown Pond has an open breachway giving access to the coastal waters of the open sound. There are relics of former breachways (Figure A-1) that connected the pond to the open sound at various locations along the barrier beach in the past history of the lagoon. The most recent relict breachway entering Central Basin is directly opposite an inland embayment, Fort Neck, that projects northerly from the central basin of the lagoon. It is assumed that this former breachway channel may have served as the inlet for ships when this pond was a seaport in the 17th and early 18th centuries.

Charlestown Pond may be separated into a Central Basin, into which the breachway enters from the sound, an extension inland from Central Basin, known as Fort Neck, and westward, parallel to the coast, a third embayment of the pond called West Basin. All three of these basins are of similar depth profile (Figure A-6). For the most part, the depth of the three basins is about two meters with some deeper areas in all three basins. Eastward from Charlestown Pond, connected by a very narrow strip of water, is Green Hill Pond. There is evidence that Green Hill Pond at one time may have been connected directly to the open sound. The bathymetry of Green Hill Pond is very similar to that of the other three basins of Charlestown Pond. However, as pointed out by R. J. Conover (1961), there are very distinct topographic and hydrographic differences between the two ponds. Presumably Charlestown and Green Hill Ponds were once a single embayment. The early charts of Rhode Island's coastal waters show this feature. Johnson (1925) points out that the barrier beach advanced shoreward and the marsh extended further into the pond area in subsequent years. As a consequence, the lagoon became smaller in size and constrictions occurred between the various basins. Only a very narrow tidal river remains today between Green Hill Pond and Central Basin of Charlestown Pond. R. L. McMaster (unpublished data) pointed out to R. J. Conover that there were two sources of sediments (see Dillon, Volume II, 1964) in the ponds. According to McMaster's account, the two sources were coarse sand, pebble and cobble of glacial origin found along the inland shore and the beach sand originating from the barrier beach and transported by repeated hurricane action and distributed along the seaward shore of the pond. The third source, as R. J. Conover indicated, is the organic-rich bottom sediments derived in part from benthic plants, reedy marsh plants, and planktonic residues mixed with the fine fractions of both glacial and beach sands and silts.

The distribution of organic carbon (Dillon, Volume II, 1964) in the pond reflects the relics of organic deposits of former living communities in the recent past and when the pond was of a much larger extent (Figure A-8). Note in the data for the bathymetry of the pond (Figure A-6) that there are only a few deeper areas and these are restricted to channels carved out by tidal currents. There are a couple of depressions in the Fort Neck embayment. These depressions are believed to be small "kettle holes" within an outwash stream valley. It is of interest that the organic content, as organic carbon, in sediments of these "kettle holes" is higher in concentration than elsewhere in the pond. One explanation is that the saltwater "wedge" meets the influx of fresh-water discharging from the two brooks at the inland end of Fort Neck (Figure A-1; KTB and CMB) and electrolytic flocculation of clays and silts takes place where there is a sharp gradient of salt to fresh-water (Rochford, 1952). Within the flocculent silts and clays, organic matter is trapped in sediments. As oxygen is rapidly used up, a deficit develops in these fine sediments and the poor porosity (see Dillon, Volume II, 1964) minimizes any further loss of the carbon as CO_2. As a consequence, the organic carbon is retained in the deposits to a considerable depth in these "kettle hole" depressions. The sediments containing the highest organic content are likewise those retaining the highest concentrations of inorganic phosphate and nitrate. There have been some reports (C. H. Yentsch, personal communication) that under very reducing conditions there may be a tendency for mineral nutrients to remain in the organic form, e.g., nitrogen as ammonia, and phosphorus as dissociated potassium phosphate, due to a lack of microbial activity or free oxygen for oxidative processes. In the "kettle holes" high concentrations of inorganic nutrients are present in the surficial sediments indicating that the regeneration cycles have gone full circle.

Sediments composed of coarse to medium sands mixed with pebble, cobble and shell are found around the margins of the pond and form sand bars near the mouth of the existing and relic breachways entering Central Basin from the sound. High velocity tidal currents are believed to have built sand bars from materials brought out of the breachway from the barrier beach deposits. It is possible that a greater portion of these bars may be deposited during intense storms (Zeigler, 1956), including hurricanes, rather than during normal non-storm conditions. The major basins have relatively fine silty sands containing some organic matter. However, the unoxidized organic matter is largely confined to the first two to five centimeters.

Most areas of the bottom of the estuary are firm and will readily support attached vegetation. The exception is in the "kettle holes" of Fort Neck embayment. Due to the flocculent silts and the development of an oozy, black sediment having poor supporting quality, the habitat is not well populated.

A survey of the nutrients in the surficial sediments was made and these data (Figure A-18) indicate that high concentrations of orthophosphate (and nitrate; data on file) are found in the rich, organic, fine-grained sediments of the major basins and the slues, whereas relatively low concentrations of nutrients are found in the medium to coarse sands and cobble, shell, pebble, and glacial till found in the shallower water of the pond margins.

The Physical Hydrography

In the earlier survey made in Charlestown Pond by Robert J. Conover (1961), the physical hydrography was described in terms of the seasonal changes in the distribution of temperature and salinity. The hydrography was related to the volume exchange, the run-off, evaporation, influx of the sea, and the effect of wind on the distribution of properties. Although the authors of the two surveys differ in their interpretations, the former worker did not have access to the additional data which alters the earlier views. Since the first survey, eight years ago, unrecorded local and climatic changes may have brought about differences. In general the two surveys do tend to complement one another.

In Figure A-4 current data are shown which provide a flow scheme of the current patterns in the estuary under the influence of a southwest prevailing wind in June during a neap tide. During a spring tide period the current increments are half again to almost double the values given here. Superimposed on the pond circulation driven by tidal currents is the effect of wind (Barlow, 1954) which will be discussed later. A strong influx of tidal water moves into Central Basin from the breachway on the flooding tide. The major portion of the tidal flow turns left and moves westward into West Basin. A certain amount of the flow moves into Fort Neck and another important fraction flows from Central Basin eastward through the tidal stream (GHCP) into Green Hill Pond. Tidal flow measurements were taken at a depth of one meter when wind velocities were less than eight knots. These data represent the main flow of of the middle stratum of the system. The use of surface drogues in the form of filter paper discs indicated that the surface waters often moved in response to the wind quite apart from the major water mass circulation in the estuary.

In Figure A-4 note that the major movement of tidal water in the lagoon is westward into West Basin where the inflowing tidal water develops a great gyre with the center indicated just a little north and west of the center of the basin. This gyre is counterclockwise on the flooding tide and clockwise on the ebbing tide. The change in direction of rotation is indicated by the lines of current flow with arrows at either end. The reason for the change in gyre direction with flood and ebb tide is believed to be due to the wind stress on the incoming or flooding tide component which would tend to move water against the northeastern shore of the basin against the Coriolis force, whereas the outgoing or ebbing tide would tend to follow the influence of the Coriolis force aided by the southwest wind.

Note that there are gyres in many of the coves and microembayments around the estuary (Figure A-4). This tendency for the development of these small gyres on both the flooding and ebbing tide results in the deposition of fine-grained sediments and entrained organic matter in many of these small embayments. With the burial of the organic matter in these high porosity silts, the sediments become highly reducing since gas exchange is limited and free oxygen is consumed. The end result is the accumulation of high organic silts containing considerable concentrations of nitrates and phosphates, ammonia, methane, and hydrogen sulfide under a characteristically low pH environment.

In Table 2 - 1 the volume exchange is shown for the tidal exchange on neap and spring tides. Exchange volumes shown are greater than those computed by R. J. Conover in his survey.

West Basin is dominated by coastal waters due to the vigorous exchange of tidal water to and from the breachway. Due to the strength of the tidal currents (Figure A-4), the embayment is subject to a considerable movement of water and the formation of a large gyre. Very little fresh run-off water courses into the basin, but an important contribution of ground water enters by springs along the northern shore. The consequences of volume exchange and the magnitude of source waters results in a highly polyhaline environment the year around (Figure A-9S/B).

Central Basin is figuratively the crossroads of the lagoon, into and out of which courses fresh-water run-off from all of the other basins and tidal water from the sound. The embayment is very polyhaline, has the largest volume exchange percentage with coastal waters of any basin, and is subject to a dynamic concourse of currents and eddies (Figures A-4 and A-5)

Fort Neck embayment has a considerable influx of fresh-water from two streams, one of which drains from School House Swamp behind the recessional moraine. The exchange of tidal water is considerable along the bottom of the basin. Due to the high bluffs sheltering the basin (see section on wind effects upon circulation), thermal-haline stratification is

TABLE 2-1

THE VOLUME EXCHANGE DURING ONE TIDAL CYCLE

IN CHARLESTOWN AND GREEN HILL PONDS, RHODE ISLAND, 1962-63, BASED ON FLOW RATES*

Embayment	Total Vol. (M^3) at MTL	Water lost (M^3) at ebb tide	Water gained (M^3) at flood tide	Net water loss (M^3) seaward
West Basin (from the narrows at Central Basin)	4,357,157	Neap: 1,417,252 Spring:@ 2,834,204	Neap: 1,417,102 Spring:@ 2,834,204	Max. 176 Min. 132
Central Basin (mixing basin for waters of all other embayments with coastal waters.)	3,253,320	Neap: 14,171,520 Spring:@28,343,040	Neap: 14,156,520 Spring:@28,313,040	Total accumulation fresh-water in all basins passing into Central Basin from springs, seepage, run-off Max. 900 Min. 150
Fort Neck Embayment	1,161,900	Neap: 7,951 Spring:@ 15,903	Neap: 7,051 Spring:@ 14,103	King Tom Brook: Max. 10,800 Min. 2,700 Cross Mill Brook: Max. 16,997 Min. 3,435
Green Hill Pond	2,207,610	Neap: 32,477 Spring:@ 64,955	Neap: 28,465 Spring:@ 56,930	Factory Brook: Max. 7,344 Min. 2,423 Tributary: Max. 20 Min. 8
Breachway to Block Island Sound		Neap: 14,171,520 Spring:@28,343,040	Neap: 14,166,520 Spring:@28,333,040	Total per cycle Max. 36,237 Min. 8,848

*Vaned drogues suspended on 1 meter wire were timed in transit over a measured course of known cross section at the entrance of each embayment. Therefore these data are corrected for wind effect.
@Estimates based on neap tide measurements.

better developed than in the other sections of the lagoon. As a consequence, a strong salinity gradient develops in this embayment. Many eddies develop around the island and indentures of the shoreline creating a complex current pattern on ebbing and flooding tides.

Green Hill Pond receives a nominal amount of tidal water exchange, run-off is considerable, and the net result is a low polyhaline environment. However, due to the narrow tidal creek through which tidal water must course, there is a narrow zone of high velocity (Figure A-4), turbulent water in the pond. The remainder of the system is sluggish with very slow moving eddies in the microembayments (note gyre symbols, Figure A-4).

In terms of the lagoon system as a whole, the spring seepage amounts to about 15 per cent of the total influx of fresh-water entering the system. Seasonal rates of evaporation show a maximum in the summer period and a minimum in the winter period varying seasonally with wind and thermal conditions (Table 2 - 2). Evaporation was highest during periods of highest winds and/or lowest humidity and lowest during periods of lightwinds and/or high humidity. The total evaporation from the pond over a year's period was about 1 meter. A maximum of 8 to 10 cm. per month and a minimum of only 1 to 2 cm. per month evaporates from the lagoon surface. The annual evaporation nearly balances the amount of direct precipitation on the lagoon's surface. The run-off is an added increment.

TABLE 2-2

EVAPORATION DATA FOR CHARLESTOWN AND GREEN HILL PONDS, 1962-63, IN CM./MONTH

Month	Amount in cm.
January	-
February	-
March	7.2
April	9.0
May	8.4
June	12.6
July	15.1
August	18.7
September	14.3
October	7.2
November	6.1
December	4.6
January	2.7
February	6.1
Total per annum	112.0 cm.

An annual water budget for the pond was computed including the inflow of fresh-water into the system minus the amount evaporated from the surface, plus the tidal water input with a slight positive net addition to the estuary. It was estimated that a large fraction of the water evaporated from the pond was fresh. The rationale for this assumption is the fact that at times when air humidity was low, salinity of the surface film of water was higher than that of water a few centimeters below the surface. Much of the fresh-water runoff tends to be transported seaward in the surface layers during light wind conditions due to the lower density of freshwater. Some theories suggest that salt is left behind in strictly evaporation processes, excluding the bursting bubble concept of Woodcock and Blanchard.

Thermal-haline Stratification:

Referring to the data given in the appendix for temperature and salinity (Figures A-9S/B and A-10S/B), there is shown a distinct thermal-haline stratification in the pond during the warmer months. By contrast, in the colder months the ponds are practically isohaline indicating no stratification. Note that those portions of the pond which are more inland, including Fort Neck and West Basin, warm more rapidly in late spring and early summer than the coastal waters. Conversely, in the fall the lagoon waters cool more rapidly than the sound (station BIS, Figure A-1). The shoal, more isolated waters of lagoons tend to follow the air temperatures since the shallow lagoon water mass is only a fraction of the coastal water mass. Also, those areas of the lagoon which are near the breachway receive the cooler (in summer) or warmer (in winter) sound water on every tidal influx differing by several degrees from the thermal environment of more remote inland portions of the estuary. This pattern is observed in the frequency polygon projections.

The fresh-water run-off influx often appears in and is carried seaward by the surface water (see seaward reflexed isotherms in Figures A-9S/B, sections A and C). Stratification is especially marked in those areas of the pond where the largest influx of fresh-water occurs (Fort Neck and Green Hill Pond), where there is some shelter from the prevailing wind (Fort Neck) and during the warmer months. Note there is also more fresh-water entering the Fort Neck section than Green Hill Pond (Table 2 - 1). The general salinity of Green Hill Pond, especially the bottom water, was generally more brackish than any other embayment in the lagoon. Rather poor thermal-haline stratification develops in Green Hill Pond due to the effects of wind mixing related to the exposure of the pond (see discussion on wind effects). Fort Neck embayment is protected by bluffs composed of moraine material, hence stratification develops and persists. The stratification permits the fresh component entering Fort Neck embayment to move seawater in the surface layer (see Figure A-9S).

Central Basin and West Basin are under the strong influence of a large tidal exchange and wind which results in moderate and rather temporary stratification. The fresh-water component from Fort Neck is flushed out of Fort Neck and into Central Basin and ultimately seaward with each tidal cycle. As a consequence, fresh-water inflow into the Fort Neck section, though significant in amount, does not critically dilute the deeper water of Central Basin. Using Ketchem's formula (also employed by Robert Conover), the estimated flushing time for Charlestown and Green Hill Pond lagoon is less than five days. This difference in opinion is probably a difference in climatic data rather than interpretation.

Up to this point our concern has been with circulation of the pond system as related to tidal phenomenon and the inflow of fresh-water. The effect of wind is a second force superimposed on the tidal pattern. Barlow (1954) decided that wind was more important than tide in effecting changes in the circulation of Great Pond Falmouth, Massachusetts. During periods of strong winds, including velocities from 18 to 25 knots which are experienced during the postfrontal passage of air masses and during storm periods, the waters of Charlestown Pond become very choppy and wave action "feels" the bottom. During such periods the entire water column structure is broken up. This event was also noted in the Great Pond Falmouth studies (Conover, 1958). The wind moves the major flow patterns, established by tidal forces, toward the windward shore during prevailing southwesterlys in Charlestown Pond.

Usually a frontal storm passes through followed by gusty westerly and southwesterly winds. In Figure A-2 note that there is a very distinct rise in the wind velocity following the passage of each low pressure trough through the region. Since these data are weekly averages, specific storm or front passage is not always singled out. The large departures from the means indicate that there was either a long or intense period of wind stress on the estuarine system. The long period wind conditions are of greater consequence than short term storms.

Several spot checks were made on the effects of wind-moderated currents during periods of strong winds. One of the most conspicuous observations was the fact that the tidal current tracks were displaced toward the leeward shores. West Basin is favored by a direct flow of tidal water from the breachway subject to turbulence on the flooding cycle due to the prevailing southwesterly wind stress against the tidal flow. This is the phase of the tide when import dissolved properties brought in from the sound are distributed within the lagoon. The entire water column tends to be disrupted under southwesterly winds exceeding a force of 15 knots. Easterlies are less common and usually of limited force. The lagoon is in the lee of the moraine from northerly winds.

In Central Basin, winds have a much smaller reach than in West Basin and there is some protection from low bluffs. The tidal control is always dominant in the circulation pattern. Unusually strong southwesterly winds tend to push Central Basin water into Fort Neck and into the eastern end of Central Basin causing upwelling along the eastern shore.

The effect of the wind on the Fort Neck embayment current pattern during strong southwesterly winds is to dampen the movement of that body of water. Currents in the ebb and flood stages tend to be lessened. There is some pressing of the flooding currents toward the eastern shore of Fort Neck since the western shore is sheltered by moraine material which creates eddying in the small embayments. The result is the development of many small eddy gyres especially along the eastern shore. These eddies tend to retard the outflow from Fort Neck.

There is a tendency in Green Hill Pond for southwesterly winds to drive the tidal current more rapidly into the central portions of that pond during periods of high wind on the flooding tide. Because Green Hill Pond receives the flooding tide water from the west in contrast to the flooding tide water entering from the east, as in West Basin, the southwesterly wind has an opposite effect on the inflow of tidal water into Green Hill than it does on West Basin. The contrast permits one to more closely scrutinize the role of the wind related to various processes in the lagoon.

The southwest prevailing wind favors ebbing and disfavors flooding tides leaving and entering West Basin. The resistance of the wind against tidal flow causes turbulence capable of mixing the lagoon waters from top to bottom and even roiling the surficial bottom silts and clays (observed by the writer during a SCUBA survey). The entraining process theorized by R. J. Conover (1961) might be inoperative under these conditions. Measurements of salinity, temperature and nutrients by ecologists are usually made during periods when there is no high wind. Stratification in the eastern half of West Basin is known to be destroyed when southwesterly winds exceed 15 knots. Properties in the water brought into the basin would be thoroughly mixed during these windy periods. Also, properties in the surficial sediments would be more easily diffused into the water column under these conditions (see Figures A-2, A-9S/B, and A-4).

The transport of substances from the muds and sediments into the water column have biological significance (Mortimer, 1941 and others). As indicated in the climatological data for winds and barometric pressure (Figure A-2), there are periods during which there are strong winds which roil the waters, "feel" the bottom and bring the surficial sediments of the estuary into suspension. The fine-grained fractions are particularly susceptible to disturbance. This fine fraction contains organic matter and mineral nutrients. Turbidity due to this fine fraction (observed by microscopic examination) rises very rapidly during periods of high wind stress on

Charlestown Pond. This action provides a very good opportunity for dissolved substances present in the latticework of silts and clays to enter the water column. The effect is not a continuous one but seasonal especially during periods of equinoctial storms in spring and fall. Occasionally nutrient diffusion from the fine-grained sediment in suspension takes place in summer during a "southwester" storm.

Lagoon evolution theory suggests that the fresh-water flow into many estuaries is largely responsible for maintaining a connection with the open sea through a barrier beach. The fresh-water influx into Charlestown-Green Hill Ponds is small, less than 5% of the total volume, and as a consequence, the role of fresh-water in helping maintain a breachway system may be relatively small. On the other hand, the tidal currents which are a function of the emptying and filling of the estuary based on a gravity system provides the maximum energy involved in carving and transporting bottom materials and in turn keeping the breachway clear between lagoon and coastal waters. There is evidence that in the past the breachway was broken along various sections of the barrier beach as indicated by the relic channels (Figure A-1) that can be seen along the marsh areas either side of the present breachway. The breachway may have been choked off completely at times in the past. Hurricanes and other storms, as well as the feeble fresh-water flow and man's efforts have been responsible for retention of the tidal lagoon system. The role of heavy storms, hurricanes in particular, has been emphasized by Zeigler (1956). If the present breachway was not occasionally dredged (see R. J. Conover's comments, 1961), undoubtedly the channel would have filled in some time ago. The lagoon may be in a terminal phase of existence as a tidal estuary. Gradually the sedimentation processes may be cutting off the coastal source of marine waters. It is the writer's belief that Charlestown and Green Hill Ponds represent a hydrographic system which persists as a tidal estuary due mainly to tidal currents rather than wind-driven or run-off currents. Finally the estuary may be in its terminal phase as a productive lagoon.

THE CHEMICAL OCEANOLOGY OF CHARLESTOWN POND, RHODE ISLAND

Introduction

Categorically we have considered the lagoon as a physical system in Section 2. Shifting our approach, let us consider the same environment as a physico- and biochemical system. From an inspection of the seasonal data for temperature, pH, Eh, and dissolved oxygen (Figures A-10S/B through A-13S/B), it is apparent that seasonally as well as spatially, from one part of the lagoon to another, there are marked differences in the distribution of values of these several parameters. These differences reflect the chemical processes which occur at various times and places in the lagoon as a consequence of varying bioproduction and the conditions for production events to occur. Although the state of the art is still short of employing data from measurements of these parameters directly in terms of the specific processes taking place, their rates and causes, some generalizations and interpretations are possible based on the work of others (Beyers, et al, 1963; Copeland, et al, 1961; Odum, 1956, 1960; and others).

The changes in dissolved oxygen vary with temperature. This general trend is clearly evident in the change in magnitude of the oxygen values which are higher in winter and lower in summer. Superimposed on the temperature effect is a noticeable decrease below saturation values, especially in the surface waters of West Basin and Fort Neck embayment, and supersaturation or enrichment values for the bottom waters of all embayments, especially in the warmer months. These effects are believed to be largely biological. The pH and Eh data tend to provide the clue to this biological activity. Low Eh or negative potential values suggest a strong oxygen demand whereas positive potential Eh values indicate a decreased oxygen demand. pH values for these same periods and places in the lagoon provide information on respiration and photosynthesis exhibiting not only the diurnal swing in metabolism (Odum, 1956) of a total lagoon community but give some insight into the seasonal and spatial effects of metabolism and physicochemical processes characteristic of each habitat.

Rather than devote space to a lengthy discussion of these changes in oxygen, pH, and Eh in the various basins and habitats and guesses as to the nature of their differences and what these differences mean, these data will be referred to in Sections 7 and 8 of this report as related to specific phenomena.

A study is still in progress correlating pH, Eh, and dissolved oxygen in lagoons and embayments as a multiple factor problem. These data summarize the physico- and biochemical consequence of events in a body of water on a seasonal basis. Conover*, following Tully and Dodimead (1957), has drawn up pH : DO ratios for all stations and plotted them seasonally

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* PhD. Thesis, 1958, in the files of the Horace Rackham School of Graduate Studies, University of Michigan, Ann Arbor, Michigan, and given in a paper before the Atlantic Estuarine Society in the spring of 1963.

(oxygen on the ordinant and pH on the abscissa). The result is a counterclockwise rotation of values of these ratios during the course of a year. In embayments with strong salinity gradients and considerable fresh-water influxes, these ratios follow fairly strict linearity from river to coastal waters. But in embayments and lagoons such as Charlestown Pond, where the coast-wise orientation and minimal fresh-water influx fails to develop an important salinity gradient, these pH : oxygen ratios present a seasaw (temperature effect) with spring and fall periods exhibiting the most drastic pH departures characteristic of these equinoctial seasons. Further elaboration on the meaning of these relationships is pending further study and experiments in this laboratory.

Other properties concerned in the chemical picture are the macro-nutrients and their seasonal distribution, sources and regeneration cycles in the lagoon. Since R. J. Conover (1961) did not consider the sources external to the system or the total effects of all plant groups in the lagoon, a reevaluation was made of the phosphorus, nitrogen, and a limited study of the silicon cycles in the lagoon during the second survey (1962-63).

Methods:

Water samples were taken at two depths, surface and near the bottom using a suction sampler (Conover, 1958) which permitted thorough flushing of the apparatus before samples for dissolved oxygen, pH and Eh were taken (O_2, pH and Eh determinations are described in Section 7). Samples for PO_4-P, total P, NO_2-N, and NO_3-N were bottled in glass stoppered bottles from the overflow water of the sampler and stored and transported in an ice chest to the laboratory.

Nitrite (NO_2-N) was determined after a method by Griess-Ilosvay and nitrate (NO_3-N) by the method of Mullin and Riley (1955). Phosphate (PO_4-P) phosphorus was determined by the Deniges-Atkins method as described by Wattenberg, further modified by Strictland and Parsons (1961). Total phosphorus was determined after Strictland and Parsons (*Ibid.*). Silicate (reactive) was determined by the Chow and Robinson method (see Strictland and Parsons, *Ibid.*).

A Dynamic Approach to Estimating Nutrient Budgets:

The usual method of determining the seasonal and annual budget of a nutrient in a body of water is to utilize the excess nutrient data as if they were proportional amounts of the actual levels which are cycled or brought into, utilized, and recycled in a system. This method, however, fails to take into account the dynamic aspects of the turnover of nutrients. In fact the most serious criticism that can be leveled at this static approach is the method's failure to account for differences in uptake or assimilation rates which vary seasonally as the thermal kinetics in the system vary. The method also does not take into account the relationship between an organism and the flow of the media which has been shown to affect metabolic rates of both plants and animals (Conover, 1965). In the dynamic approach the data for the static nutrient cycles for the year are converted to dynamic levels. The conversion is a matter of weighting the static data with respect to some important variables in the habitat including flow rates of the medium and temperature effects.

Making the assumption that there are more nutrients available to plant tissues in habitats where strong currents occur, it is possible to adjust static data based on experimental data. Since we are dealing with nutrient excesses, we must remember that these excesses serve only as an index of the proportions of the total amounts present in the system. Sometimes one can measure no nitrate or phosphate. This does not mean that these nutrients are not present for utilization.

Rather, this means that there are no excess ions to be measured. Probably the recycle rate is so rapid during these periods that there are no free ions to be detected. Studies by Hood, et al (1959) support this interpretation.

In an analysis based upon these principles, an estuary should be delineated in terms of current regimes representing areas of quiet to more rapidly moving waters. For every increment of increase in current in a habitat during a tidal cycle, the amount of nitrate or phosphate statically measured should be increased proportionately. This method provides for metabolic increase and the concomitant uptake increase, both passive and active, which actually does take place in attached plants.

A tumbling stream which enters a lagoon contains a certain concentration of a nutrient, say it is one of the important sources in our model. The amount of a nutrient per volume per time can be computed and an estimate made of the total amount of this ion entering the estuary from the source. If one computes the flushing time of the system based on volume exchange, then obtains the amount of a nutrient that passes from all external sources into the lagoon, it is possible to summarize all source contributions and obtain a realistic absolute amount of a given nutrient which may pass through the system for a given period. Using these estimated values to represent the phosphorus and nitrogen supplied from outside sources, an estimate can then be made for the entire lagoon for a given period. This estimate should be of the same order of magnitude as the dynamically adjusted nutrient values with the omission of the amount of a nutrient recycled in situ. To obtain the ih situ regenerated fraction, one must depend on the residual remaining after all other source contributions have been accounted for. However, unless the dynamic approach is used in obtaining the monthly values, the recycled fraction will be seriously underestimated. If this is a valid concept, the standing crop should reflect the static proportions and the gross production rates should parallel the dynamic proportions of the nutrient supply actually being cycled at any moment.

The organic carbon (see section 4), measured in the bottom sediments, should provide information relative to the distribution of organic units in the system in the recent past history of the lagoon. These data should show proportionate production amounts per spatial distribution, in terms of organic carbon. The organic carbon residues in the surficial sediments give the long period average from decades to several centuries. All of these approaches: the utilization of raw materials; the recycling of essential macronutrients; the loss of some fraction by flushing to the sea; and attrition by storm action should match in order of magnitude. Once fitted together, the budget of a marine estuarine system of unknown capability might be computed and the progress or fate of the system predicted.

What correction should be used to magnify the static residuals of the nutrients normally measured in an estuary? The writer proposes a system which is based on metabolism experiments with algae and aquatic phanerogams (Conover, in this volume). For a 5 cm./sec. flow rate, the factor should be 2.5. For a 10 cm./sec. flow rate, the values are doubled or 5. Every time one doubles the flow rate, the absorption rate is doubled. For a one knot, or 52 cm./sec., current, the potential absorption rate is 25.

Considering the thermal kinetic side of the picture, the well-known principle may be applied that for every 10°C increase for the thermal kinetics in the system, there should be a doubling of the rate of reaction. In biological systems, the enzymatic patterns give higher rates for given kinetics at high efficiency levels. However, to retain the simplicity of concept required of our model, the correction for temperature should only permit the escalation of values of recycling in accordance with the kinetic law for physico-chemical reactions. As the season progresses, the water warms up and the available amount of nutrients becomes recycled more rapidly. Ultimately the recycling is so rapid (Hood, et al, 1959) that NO_3-N and PO_4-P are "statically" undetectable in some portions of some lagoons, yet there is enough P and N to sustain high bioproduction rates. The dynamically adjusted values should give a more realistic estimate of the amounts of the nutrients available which are absorbed, utilized, and recycled annually in a lagoon. Instead of dealing with mere proportions, there is hope of dealing with finite amounts of nutrients cycling in a living community.

The Nitrogen Budget:

By interpreting nutrient data with an emphasis on the thermal and fluid motion kinetics, the following picture unfolds for the annual nitrogen budget in Charlestown Pond. From the data, it is evident that there is a great deal of variability in nitrite and nitrate with the seasons. Ammonia was not measured, but may be estimated on the ratio of 5:1 from these two measured fractions. The lack of ammonia data is an unfortunate oversight.

The neritic water as a nitrogen "source" is apparently more important to Charlestown Pond, Rhode Island than it is to Great Pond Falmouth, Cape Cod (Conover, 1958). The run-off contribution to Charlestown Pond is less important than it is for Great Pond. Since the neritic water source together with the fresh inflowing water source contains much less nitrogen (NO_2, NO_3) than the total amount present at any one time, there is evidence that in situ recycling of nitrogen may be the primary immediate source of nitrogen in this system. Whether or not this is meteoric nitrogen or a gradual accumulation from neritic and fresh-water run-off sources is not known. Probably all three of these origins are involved.

In some seasons of the year, concentrations of nitrite and nitrate were below detectable levels, while during other seasons concentrations were very substantial (Figures A-14S/B and A-15S/B). The pulses of nitrite and nitrate were not synonymous in time or place in the pond. There was some indication that recycling processes were taking place which were reflected first in the formation of nitrite, followed by nitrate.

In a brief span of time, large fluctuations in nitrate concentration occur at some stations. In terms of spatial distribution, there are areas in the pond characterized by low values, while at the same time other areas exhibit moderate or high values. This situation may be due to differential metabolism by plant communities in different parts of the lagoon. Differential metabolism is a reasonable assumption in view of the observation that areas where concentrations of nitrate and nitrite were low in Charlestown Pond corresponded with those areas where phytobenthon and phytoplankton production was high.

The data show that there are periods in which relatively sharp changes from high to low concentrations are observed: e.g., the period from October to November, and also from July to August. There are also periods of relatively low concentrations in April to May, June, July to August, and December to January. Looking at the data for the month of May, note there are lower values in the larger open basin where plant production is high. As the seasons progress, there is an increase in concentration (above 1 μg.at./L.) of nitrate or combined nitrate and nitrite in the open basin which is very striking in May and June. In July values plunge as metabolism rises rapidly with the increase in thermal kinetics with the approach of the thermal maximum of the year. By way of explanation it is necessary to picture the benthic community as actually dominating the surface, middle, and bottom waters in the lagoon because the blades of the immergent sea grasses are so tall they actually float at the surface in many of the productive areas of the pond. Consequently it is not surprising to find that, in spite of salinity thermal stratification which is strongest in the warmer months in the lagoon, the surface and bottom water values of nitrite and nitrate at times show a distinct parallel. This condition suggests that the nutrient uptake by benthic plants is equal in surface, middle and bottom waters. Where there are very dense stands of benthic plants, some measurements indicate that there is a much greater parallel in concentrations throughout the water column in contrast to areas where there is a fairly good bottom growth of those plants which do not extend into the surface waters. Phytoplankton populations are apt to be more abundant in the latter habitats.

In terms of what is happening in the lagoon during the thermal maximum of the year, this period may be one of the most interesting to examine in the light of the attempt to characterize the dynamic qualities of nutrient cycles in a lagoon. Turning our attention to the data for nitrogen during the month of August, there is a marked regeneration period. This same phenomenon was noted in Great Pond Falmouth, Cape Cod for the same month. Note that the thermal kinetics (Figure A-10S/B) of the water are highest at this time. The bottom water nitrate is fairly low in the open basin and areas of high production of plants. In the surface water there is more nitrite, but in terms of the entry of nitrite from the source areas, there is more nitrite entering from fresh-water sources but relatively little entering the bottom water from in situ sources at this time. One is tempted to interpret this situation in static terms as a period in which nitrate might have been limiting to plant growth.

Using dynamic data adjustments, quite a different picture is obtained. Temperature has increased (Figure A-10S/B) and probably obtained the highest thermal level for the year; current patterns are present and will increase the metabolic rate uptake recycling. Also, moving water (Figures A-4 and A-5) will be carrying more nutrients from the external sources into the estuary. One could expect that the nitrite entering from fresh-water sources may be in the process of being converted to nitrate in the surface waters and in turn is being partially flushed to sea in the fresh component with every ebbing tide. A certain fraction of the in situ regenerated nitrogen is also flushed to sea. Volume exchange data permits an estimate of the amount lost with each tidal exchange by prorating the stroboscopic data (see following discussion).

Calculations for the Nitrogen Budget:

The nitrogen budget in Charlestown-Green Hill Pond is based upon biweekly data, but these data are considered in a somewhat different light than is usual for such seasonal estimates: namely, the data are considered stroboscopic. The use of this term in this context is to visualize the values measured as the instantaneous value of concentration of a substance in sea water considered as resultant of all the dynamic processes that contributed to its existence at that moment. If the measurement was repeated at intervals within days of the time actual measurement was made, it is assumed that the value would be approximately the same. A value visible only at intervals, especially if periodic, is stroboscopic. Hence, each biweekly measurement is a stroboscopic representation of the value over a two week period. The annual total is a stroboscopic sum of all of the biweekly values. The finite amount present in a continuous sense in time and space is undoubtedly greater and can only be inferred (see discussion under nutrients in section 7). In Table 3-1 are data for the sources and the major basins of the lagoon on an annual basis. Since these totals are the sum of the biweekly measurements, they represent stroboscopic totals and not finite totals of nitrogen in the system. The proportions are real. The concentration values are the result of a semi-steady state condition at each measurement period, hence, differences in the annual totals should reflect real differences in the budget turnover in each basin or embayment. Table 3-2 shows the individual budgets for each basin or embayment.

TABLE 3-1

THE STROBOSCOPIC ANNUAL NITROGEN (NO_2,NO_3) BUDGET IN CHARLESTOWN AND GREEN HILL PONDS, RHODE ISLAND IN 1963

Source	Annual Amount μg.at./L.
All springs and run-off	4.40
King Tom, Cross Mill, Factory Brooks (dilution 4x) . . .	36.35
Block Island Sound	16.70
*From *in situ* regeneration . . .	85.12
Total	142.57

Lagoon Basin	Annual Amount μg.at./L.
Central Basin	52.43
Green Hill Pond . . .	25.98
West Basin	41.35
Fort Neck Embayment	22.81
Total	142.57

*Amount remaining not accounted for from other sources

TABLE 3-2

NITROGEN BUDGET (NO_2,NO_3) FOR EACH BASIN AND EMBAYMENT OF CHARLESTOWN AND GREEN HILL PONDS, RHODE ISLAND IN 1963.

Source	Annual Amount μg.at.N/L.	Total NO_2,NO_3 in Basin	Annual Amount μg.at.N/L.
West Basin			
Springs, seepage, and run-off	1.50	Nitrite-NO_2	4.93
Brooks	0.00	Nitrate	36.42
Block Is. Sound coastal waters	5.00		
In situ regeneration and entrainment	34.85		
Annual total	41.35	Annual total	41.35

TABLE 3-2 (cont.)

Source	Annual Amount μg.at.N/L.	Total NO_2,NO_3 in Basin	Annual Amount μg.at.N/L.
Fort Neck Embayment			
Springs, seepage, and run-off	1.50	Nitrite-NO_2	2.64
Brooks	14.35	Nitrate-NO_3	20.18
Block Is. Sound coastal waters . .	3.00		
In situ regeneration and entrainment . .	3.97		
Annual Total	22.82	Annual Total	22.82
Central Basin			
Springs, seepage, and run-off	0.40	Nitrite-NO_2	4.97
Brooks	10.00	Nitrate-NO_3	47.46
Block Is. Sound coastal waters . .	5.70		
In situ regeneration and entrainment . .	36.33		
Annual total	52.43	Annual total	52.43
Green Hill Pond			
Springs, seepage, and run-off	1.00	Nitrite-NO_2	2.52
Brooks	12.00	Nitrate-NO_3	23.46
Block Is. Sound coastal waters . .	3.00		
In situ regeneration and entrainment . .	9.98		
Annual total	25.98	Annual total	25.98

From these data it is apparent that much of the available nitrogen required for plant growth comes from fresh-water run-off or _in situ_ regeneration within the lagoon. Only a small fraction is derived from the coastal waters. Since Great Pond data (Conover, 1958) show an even stronger tendency for terrestrial sources (and meteoric sources supertend the terrestrial sources) to be predominant, there is a definite indication from these two surveys that along the southern New England coast in this region coastal waters may receive a large share of their nitrite and nitrate supply from rivers, creeks, and run-off waters from the land.

One must recognize the importance of regeneration processes in restoring nitrogen to the cycle of plant growth. According to these calculations (Table 3-1), there is 72.74 μg.at. N/L. not accounted for from any other source which must be derived from _in situ_ regeneration. See below for a further discussion of regeneration.

To estimate recycling rates at any one time of year in any particular place in the lagoon, the writer suggests two corrections if the data are at hand: 1), a correction for thermal kinetics; and 2), a correction for water movement kinetics. There is a method whereby this approach may be checked using primary productivity data (gross production of phytoplankton and phytobenthon) obtained the same day or season.

Assume one measures 2 μg. at. N/L. of nitrate at a station. The temperature of the water is 20°C. Using the well-known relationship that a reaction, oxidation-reduction, etc., (physicochemical) will double its reaction rate with every 10°C. increase in temperature, then at 20° the recycle rate will quadruple from the steady state value for a given period of time. If one uses 2 μg.at N/L. and if the temperature is 20°C. and the current velocity is 20 cm./sec., there will be 80 μg.at. N/L. effective concentration available to the plant tissues. From this scheme it is now conceivable that with high current velocities of a knot or more, actual upper limits of tolerance to some ions and molecules for some plants may be attained resulting in reduced metabolism.(Table 3-3).

In Section 8, this study is pursued further to show how the order of magnitude suggested by these computations and their respective correction parameters are reasonable in terms of the amounts of nitrate and phosphate which must be cycled in the system to support the extensive plant communities of the lagoon.

From the data shown in the frequency polygons (Figure A-14 and A-15), one can observe that there is a genuine seasonal accumulation increasing in spring, followed by a heavy utilization in early summer, and then another shorter period of accumulation. In August and September there is a period during which low values appear as if this was a period of especially heavy utilization. November and the latter part of October are marked by a distinct period of increase. During the winter months there are fairly high values of nitrate in the system.

TABLE 3-3 A,B

A. SUGGESTED TEMPERATURE EFFECT ON REGENERATION OF NUTRIENTS

Initial Amount g.at./L.	0°C.	10°C.	20°C.	30°C.
1.0	1.0	2.0	4.0	8.0
2.0	2.0	4.0	8.0	16.0
3.0	3.0	6.0	12.0	24.0
4.0	4.0	8.0	16.0	32.0
5.0	5.0	10.0	20.0	40.0

B. CURRENT VELOCITY EFFECT UPON NUTRIENT UPTAKE BY PHYTOBENTHON

Initial Amount g.at./L.	Increase in available nutrient in g.at./L. with increase in velocity in cm./sec.			
	0cm./sec.	5cm./sec.	10cm./sec.	20cm./sec.
1.0	1.0	2.5	10.0	20.0
2.0	2.0	5.0	20.0	40.0
3.0	3.0	15.0	30.0	60.0
4.0	4.0	20.0	40.0	80.0
5.0	5.0	25.0	50.0	100.0

The surface water nitrate-nitrite values often parallel those in the bottom water. The rise in nitrite a week before the rise in nitrate, especially in midsummer and again in autumn, strongly suggests marked *in situ* regeneration is involved in the nitrogen cycle in Charlestown Pond. The seaward trend of the contours enveloping low concentrations of nitrate suggest that coastal waters are a poor source and may be fed nitrates largely by lagoons such as Charlestown and Green Hill Ponds. Undoubtedly nitrates and nitrites enter the lagoon seasonally from fresh-water run-off. There is only a small influx of some nitrate from the sound. Since there is no distinct contrast of concentrations between surface and bottom water, one is tempted to draw the conclusion that nitrate and other nitrogen (NO_2, NH_4) fractions may originate *in situ*. If not, bottom water should generally be richer in nitrate compatible with the coastal water source of the bottom water. If there are relatively higher amounts of nitrite present in Central Basin, West Basin, and Fort Neck, this might strongly indicate a high degree of regeneration and imply important recycling patterns there. This is, of course, of the basis of first assumption of over-all appearance of the frequency polygon data. The implication from the earlier survey by R. J. Conover (1961) was that less nitrate was available to plant organisms in West Basin than in either Central Basin, Fort Neck, or Green Hill Pond. The second survey data indicates that West Basin has just as much nitrate seasonally as the other basins. Although the fresh-water run-off does have high concentrations of nitrate much of the year, these are diluted in the exchange by 4 times or more. All of the embayments have equivalent amounts cycled, accumulated, and utilized seasonally. There is a very distinct correlation between the seasonal oxygen deficit in the system and regeneration cycles of nitrate, nitrogen. Undoubtedly oxygen uptake is being diverted for in situ regeneration purposes, hence strengthening the arguments in favor of a strong regeneration cycle. The other half of the same picture is indicated in the pH data. The presence of low pH values during the same periods of oxygen deficit suggests regeneration processes were in progress.

Adjustment of the Nitrogen Budget:

The stroboscopic values given in the frequency polygons (Figures A-14 and A-15) should be adjusted for each habitat and season by converting the data according to the following table. The reader should prepare a two cycle semi-logarithmic graph (K. & E. # 358-61) with the nitrate values entered on the logarithmic ordinate axis and temperature and current entered on the abscissa. Any value in any habitat of nitrate given in Figure A-15S/B can then be adjusted with the temperature data in Figure A-10S/B and with current velocity in Figures A-1, A-4, and A-5 (Table 3-3).

The results show a fairly constant lunar periodicity for current throughout the year but the temperature effect will change with the seasons. When the thermal kinetics are high, metabolism nutrient demand and nutrient recycling will be high. A realistic, if stroboscopic, estimate of the dynamics of any habitat can be evaluated in this way.

The Phosphorus Budget:

Phosphorus and nitrogen cycles are not similar in this lagoon but follow independent patterns of seasonal change. The distribution of inorganic phosphate in the lagoon, similar to nitrate, appears in surface and bottom water in the same sequence of high and low concentrations during the same periods (Figure A-16S/B). The sources of inorganic phosphate in the estuary are the same as those for nitrogen: (1) fresh-water run-off from the land, especially creeks and brooks; (2) the neritic coastal waters entering through the breachway; (3) the *in situ* regeneration within the lagoon; and (4) from the surficial sediment by diffusion (Tables 3-4, 3-5).

The bottom water does retain higher concentrations however. According to R. J. Conover (1961), this phenomenon was due to the nature of the two-layered thermal-haline system which concentrated nutrients brought in by tidal waters. This mechanism could be operative, but the importance of this process may not be as great as the originator of this idea believed. Included in his entrained fraction was the quantity of orthophosphate regenerated *in situ* and the fraction which may be diffusing out of the sediments roiled by strong winds.

As with nitrate, phosphate also accumulated seasonally in 1963 as one can observe in the frequency polygon projections for inorganic phosphate (Figure A-16; note especially sections B and C). It is evident from these data that seasonally there are periods of low alternating with high concentrations non-uniformly throughout the estuary. With the exception of June,

TABLE 3-4

THE STROBOSCOPIC ANNUAL PHOSPHATE (PO_4) BUDGET IN CHARLESTOWN AND GREEN HILL PONDS, RHODE ISLAND IN 1962-63.

Source	Annual Amount µg.at./L.	Lagoon Basin	Annual Amount µg.at./L.
All springs and run-off	4.11	Central Basin	46.56
King Tom, Cross Mill, Factory Brooks (dilution 4x) . . .	5.02	Green Hill Pond . . .	3.46
Block Island Sound	13.85	West Basin	11.31
*From in situ regeneration and entrainment	68.96	Fort Neck Embayment	30.61
Annual total	91.94	Annual total	91.94

* Amount remaining not accounted for from other sources

TABLE 3-5

PHOSPHORUS BUDGET FOR EACH BASIN AND EMBAYMENT IN CHARLESTOWN AND GREEN HILL PONDS, RHODE ISLAND IN 1962-63.

Source	Annual Amount PO_4-P µg.at.P/L.	Total PO_4,T-P, Dissolved-P in Lagoon Basin	Annual Amount µg.at.P/L.
		West Basin	
Springs, seepage and run-off	2.11	PO_4-P	11.31
Brooks	0		
Block Is. Sound coastal waters . .	4.30	Dissolved and Particulate organic P_2O_5-P	72.10
In situ regeneration and entrainment . .	4.90		
Total	11.31	Total	83.41

TABLE 3-5 (cont.)

Source	Annual Amount PO_4-P µg.at.P/L.	Total PO_4,T-P Dissolved-P in Lagoon Basin	Annual Amount µg.at.P/L.
		Fort Neck Embayment	
Springs, seepage, and run-off	0.50	PO_4-P	30.61
Brooks	4.22		
Block Is. Sound coastal waters . .	2.50	Dissolved and Particulate organic P_2O_5-P	72.67
In situ regeneration and entrainment . .	23.39		
Total	30.61	Total	103.28
		Central Basin	
Springs, seepage, and run-off	0.50	PO_4-P	46.56
Brooks	0		
Block Is. Sound coastal waters . .	6.55	Dissolved and Particulate organic P_2O_5-P	104.33
In situ regeneration and entrainment . .	39.51		
Total	46.56	Total	150.89
		Green Hill Pond	
Springs, seepage, and run-off	1.00	PO_4-P	3.46
Brooks	0.80		
Block Is. Sound coastal waters . .	0.50	Dissolved and Particulate organic P_2O_5-P	15.83
In situ regeneration and entrainment . .	1.16		
Total	3.46	Total	19.29

July, and early August in all sections of the estuary, there were no important differences between surface and bottom values. In the warmest months in West Basin, the bottom water retained high values while immediately above in the surface water, low values persisted suggesting that a two-layered system was in effect at that time. However, stratification was never well-developed in West and Central Basins except in midsummer during conditions of light southwesterly winds.

In studying the trend of the isopleths, especially in the bottom water, there are changes in time showing concentrations that start high at one time but diminish as time progresses. During a month's period, these isopleths sloped from up estuary to the right and seaward with time. This trend in the data suggests that concentrations of PO_4-P were being regenerated and then utilized in situ in the water column. If the PO_4-P was derived from an outside source, the contours would not appear as more or less closed configurations. In other portions of the figure, where the isopleths run the full length of the figure to the source, an external source is inferred. In these instances one would expect outside sources to be more important.

The importance of the various sources differ from those for nitrogen. R. J. Conover (1961) had interpreted his data to indicate that phosphorus was largely provided from coastal waters through the breachway. He drew this conclusion from the correlation he obtained between salinity and phosphorus. Referring to the frequency polygon for 1963 data for inorganic phosphate for section A, B, or C (Figure A-16S/B), one will notice that there is a contribution of orthophosphate emanating from the breachway from Block Island sound. These influxes of inorganic phosphate were pulsing into the lagoon from May through July. Also, there are winter entries of PO_4-P. The influxes of orthophosphate are periodic, not constant throughout the year.

If one considers the fresh-water run-off source for phosphorus, there is only a small contributionof phosphate coming from the brooks. If one considers the total phosphorus (Figure A-17S/B), there is a marked fresh-water stream transport of total phosphorus into the estuary which includes a fraction other than PO_4-P entering the pond. These data imply that the phosphorus is either organic in the dissolved form, P_2O_5-P, or is phosphorus still bound in the form of plant or animal tissues. These fresh-waters are rather poorly populated with living fresh-water organisms. The turbidity is always very low which suggests that the phosphorus is in the dissolved form as organic phosphorus or orthophosphate.

In Tables 3-4 and 3-5 estimates for the annual phosphorus budget are given based on volume exchange computations. To account for the exchange of phosphorus (or any other property) from basin to basin on the tidal cycles, the exchange fraction is included in the "in situ and entrainment" fractions.

From these data one will note that the phosphorus budget in essence is essentially in agreement with R. J. Conover's (1961) analysis of this property.

Corrections for the phosphorus budget:

To obtain estimates for phosphorus recycling, the factors used for nitrogen (Table 3-3) are applicable since both properties are subject to the same dynamic principles. It would appear from the data (Figures A-16S/B and A-17S/B) that phosphorus is more dependent on regeneration in situ in the lagoon than is nitrogen. The sustained high amounts of total phosphorus in the lagoon during the warmest months strongly indicate a high renewal rate which is not demonstrated in the influx of coastal or fresh-water run-off, springs and brooks (Figure A-16S/B). In Section 8, a comparison of the N and P budgets, estimated using the corrections for thermal and motion kinetics as related to the total demand of the plant community, demonstrates the importance of these corrections in terms of the proper order of magnitude for a reasonable cycling of inorganic nutrients.

The silicon budget:

No detailed account of a silicon budget was attempted due to the paucity of data. Seasonal data were obtained in another study, but only for the Fort Neck embayment. It is regrettable silicon analysis was not expanded to the rest of the Charlestown Pond complex to relate silicon to the growth of phytoplankton populations. From the data given in Figure 3-1, the source of silicon is readily apparent from the seaward-dipping isopleths which indicate that the influx of the property originated on land and was carried by the fresh-water effluent. Sporadic and intense blooms of phytoplankton in Fort Neck (Figure A-19S/B), not typical of the other basins, were compared with fresh-water influxes of nutrients (see Sections 7 and 8). Silicon limiting to planktonic or benthic growth (even Zostera and Ruppia include silicon in their tissues as an essential but not clearly understood functional component) is discussed in Section 8. The thermal and motion kinetics are assumed to apply to silicon as well as to the other properties discussed above.

THE CARBON CYCLE

A simplified carbon budget for Charlestown Pond is computed from data on hand for the bulk of the living biomass from estimates of the products of degradation and from the organic residues, as organic carbon, in the surficial sediments of the lagoon.

The estimates for the annual total living biomass carbon content are shown in Tables 8-5,6,7,8,9.* There is approximately 20 per cent of the total carbon unaccounted for due to a lack of complete data on the living biota (see Section 1-1). Estimates for the amount of carbon as a fraction of the total dry weight of living organisms was obtained from Vinogradov (1954).

To account for the annual biomass requirements of other essential constituents, including phosphorus, nitrogen, and silicon, the additional fractions of these constituents, related to the annual total dry weight of organisms, was computed using data from Vinogradov (*Ibid*.). Fortunately, these data for the benthic plants were obtained from plants growing in Rhode Island waters, providing some additional credence to the estimates. From these data (Tables 8-5,6,7,8,9), one can refer to the phosphorus, nitrogen, and silicon budgets, discussed at length in Section 3 and elaborated on in Section 8, in terms of finite requirements of the biomass *per annum*. The implications of these additional data are to emphasize the value of the dynamic computations suggested for correcting *in situ* regeneration values of any nutrient for the lagoon.

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*Note all Tables for this section are given in Section 8.

The difference between the stroboscopic or proportional values of available nutrients (Tables 3-1, 3-2, 3-3, 3-4) and the finite total carbon annual values (Tables 8-5 through 8-9) are thus resolved. Also, the total annual turnover of the essential constituents, C, P, N, and Si (to which H and O can easily be added by computation) can be estimated.

The presence of organic residues in the surficial sediments, as organic carbon (Figure A-8), emphasizes the fact that the cycle of elements, which are essential components of living organisms in the lagoon, are recycled at a considerable loss. In other words, the amount of basic matter entering the living system is considerably greater than the amount used to make up tissues and organs. Only a fraction of that matter constituting the degradation products of dead organisms is recycled and used again as constituents of new living generations of marine life in the estuary. The principle here has been known for a long time in ecosystems. However, the evaluation of the proportions of matter cycling in a given system, including this kind of data, are scarce in the literature. In Tables 8-10,11 an evaluation has been attempted for Charlestown Pond. The evaluation rests upon the organic content of the detritus as a measure of cycling losses.

These organic residues represent past bioproduction degradation products which were not recycled, but trapped or entrained as organic residues in the surficial sediments. The organic carbon data represent many seasons and years of accumulation within a relatively small laminar sedimentary profile of a few centimeters. These data are very useful as an estimate of the losses from carbon cycles if the period of lapsed time can be determined.

The record of past hurricanes is detectable in the sediments of West Basin in the form of tongues of sand interleaving between the accumulation of finer-grained, silty, clayey sands which slowly increase during normal non-hurricane periods. The 1832, 1938, 1954, and 1960 hurricanes can be identified in the basin sediments. Since 1954, there has been an accumulation of 5 millimeters of finer-grained sediments at the margin of the hurricane-produced sand lens, which "tongues" into the finer-grained, organic-rich sediments of the basin. The 1960 hurricane ("Donna") left its trace in the basin as a more seaward disposed sand wedge. Hurricane "Donna" did not invade the innermost border of the sandy shoals of the basin (see dotted line, Figure A-4 and the 0.5 meter isobath in Figure A-6) but may be seen as a distinct burm between the beach shore of West Basin and the 0.5 meter isobath. The 1954, 1944, and 1938 hurricanes apparently left sand wedges landward of the 0.5 isobath, hence the record of accumulated non-storm, finer-grained, organic-filled sediments which lay over these interleaving hurricane-produced sand bars represents the true accumulation of organic residues lost from the carbon and other cycles during the periods between storms.

Assuming that these layers of organic sands bear the dates of these past storms, the loss of C, P, and N per year can be calculated. Work on these calculations and interpretation of these data are still in progress at this time.

In Dillon's account (Volume II, 1964), the role of physical processes related to the deposition of organic matter was considered, but the biological phase was not. Although mechanical processes did contribute in part to the ultimate distribution of the organic carbon, present centers of bioproduction closely correspond with centers of past organic carbon deposition (Figures A-8, A-18 through A-24). Since the physical processes which affect the distribution of biological properties argue favorably for little or no change in position of organic residues from the loci of origin, it is assumed that these deposits of organic matter are autochthonous.

At the present time, as noted in Figure A-14, the benthic populations of sea grasses and algae in Charlestown Pond correspond with the location of the highest organic carbon concentrations in the surficial sediments. Concentrations of inorganic phosphate (Figure A-18) in the surficial sediments also occur in patterns of distribution identical to that of the organic carbon for the same reasons. With the exception of the "kettle hole" deposits in Fort Neck embayment, areas of highest tidal current flow, inorganic phosphate content, maximum plant biomass distribution, and the presence of the highest concentrations of organic matter all coincide. The writer proposes on this evidence that over the past hundred years of community succession, the attached plants and other members of the community have occupied nearly the same site in the estuary as they do at present. It is also evident that bioproduction has been sustained during this period at a high level.

From the evidence that the in situ deposits of organic residues in the sediments are the autochthonous remains of past communities, these residues represent both phytoplankton phytobenthon, zooplankton and zoobenthon which have been entrained in the sediments. There is a more likely chance that plankton-derived carbon was released as carbon dioxide and hexicelluloses earlier in the cycle, while phyto- and zoobenthon may be much better represented in the sediments as lignins and waxes. Hypothetically, the organic matter in the sediments may be considered as originating largely from benthos. It follows that perhaps much of the loss of residual organic matter in a lagoon may be due to that fraction of the benthos which becomes entrained in the sediments and never recycled in the living community. An additional lead is the fact that the P:C:N ratio in the surficial sediments (Table 8-2) is more nearly that of the PO_4-P:NO_3-N ratio present in lagoon waters. The meaning of this ratio is explained in Section 8.

Organic carbon is also distributed where there are no high concentrations of benthic plants in the lagoon. In particular, concentrations of organic carbon occur in the "kettle holes" in Fort Neck embayment. Dillon (Volume II, 1964) gave one interpretation of why "kettle holes" might be settlement basins. The present authors offer two other alternatives. (1) The organic matter might have been entrained in the sediments by the electrolytic process of silts and clays flocculating in the presence of a steep gradient of salinities (Figure A-9S/B) where fresh-water flows into a saline lagoon (Rochford, 1951).

(2) If one looks at the chlorophyll a data (Figure A-19S/B), one finds that there are seasonally very high standing crops of phytoplankton present in the "kettle hole" region of Fort Neck embayment. The unpublished zooplankton data of R. J. Conover show increasing populations of zooplankton cropping on the blooms of phytoplankton. The organic residues accumulated in these sediments probably represent phytoplankton rather than phytobenthon.

A combination of the two processes mentioned above could explain the particularly rich deposit of organic residues in the Fort Neck embayment. Unfortunately omitted in the survey, but not to be neglected in the future, were the eddy deposits along the shore and micro-embayments of the estuary. These eddy deposits include very high concentrations of organic matter forming organic oozes of several decimeters in depth. These organic oozes represent additional entrained losses of matter from the carbon and other cycles. These eddy deposits are strictly the result of mechanical deposition rather than biological activity and are considered allochthonous in origin. These eddies are small areas where fine-grained materials settle out into small gyres. These deposits represent an important reservoir of microorganic nutrients which tend to enrich the lagoon waters seasonally. However, the loss of organic matter in the gyres is probably much greater than that fraction which may be recycled.

Other New England lagoons with carbon cycle characteristics which are similar to those of Charlestown Pond may be expected to exhibit similar orders of magnitude. Our model has shown that a cool temperate, highly productive lagoon and the processes which are responsible for sustained production can be measured in terms of carbon. However, with more refined techniques and field experiments and the use of gas chromatography and CO_2 analyzers for more rapid and accurate carbon determinations, further elaboration of carbon cycles of lagoon waters as a clue to bioproduction should be pursued.

In Section 8 an attempt has been made to analyze the proportional contribution of each major trophic group (for which there are data) in the lagoon in terms of organic carbon (see Table 8-5 through 8-11 and discussion on page 8-13).

THE IMPORTANCE OF NATURAL DIFFUSION GRADIENTS AND TRANSPORT OF SUBSTANCES RELATED TO BENTHIC MARINE PLANT METABOLISM[1]

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Benthic marine plants grow more luxuriantly in the current tracks than in quieter waters (Conover, 1958, 1964). In turbulent coastal waters they form communities that differ markedly in species composition from lagoon communities. Algal species commonly found in open, exposed coastal waters are seldom if ever found in quiet lagoon areas. The reverse situation is also true for some species populations.

There is some evidence that differences which characterize plants and animals which occupy one type of habitat rather than another are largely metabolic. Feldmann (1937) and Funk (1927, 1954) have emphasized that rocky, open coastal lithophilic plants grow best in turbulent waters, presumably because of the high CO_2 and O_2 content of the water. Plants with high metabolic rates might flourish in such turbulent habitats but languish or never develop in more quiet waters. Odum (1956) described the higher productivity of stream communities than of quiet water communities. Odum and Hoskin (1957) found that in microcosms greater metabolism was correlated with greater stream flow and concluded that individual plants in aquatic environments metabolized more rapidly at

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[1] This study was supported by NIH grant WP-00023 and a Rockefeller grant.

higher current velocities. Fox, Simmons and Washburn (1935) discovered a similar relationship for current-adapted animals. Conover (1958) reported enhanced growth of benthic marine plants along tidal current tracks. He postulated that more inorganic phosphate and nitrate and other micronutrients might be made available to attached plants per unit time in more rapidly moving water. Blum (1956, 1962) reviewed the literature on the enhancement of river algae related to currents and demonstrated that only certain species are current-adapted.

McConnell and Sigler (1959) attempted to assess natural diffusion rates of gases and dissolved substances in a mountain stream from changes in tablet weights with time. They noted that turbulence increased the diffusion rate irregularly whereas laminar flow produced more nearly constant rates of diffusion. Schumacher and Whitford (1965), Whitford (1960), and Whitford and Schumacher (1961) assumed that the effect of current on algal growth was due to the action of the current sweeping away material near the cell surface and producing a steep diffusion gradient. The process is still ill-defined because only a few studies have been concerned with the diffusion of substances in aquatic plants. The bulk of diffusion studies has been largely restricted to terrestrial plants (Steward, et al, 1959).

The present study is directed at a reevaluation of diffusion processes in aquatic plants in an attempt to analyze further the processes related to transport rates of the medium, sea water.

METHODS

Laboratory experiments were carried out to evaluate the role of water movement on the metabolism and growth of *Zostera marina* L. and to study the processes of transport and diffusion of substances from sea water in and out of plant tissues.

A dynamic-flow incubator in which temperature, light, salinity, hydrostatic pressure, fixed initial nutrient supply and flow rate were controlled (Conover, *et al*, 1963) was used to obtain gross and net production rates of *Zostera marina* under various flow rates in a recirculated sea water microcosm. A dozen plants were processed in each run of the experiment in a 20-liter capacity system from 4 to 48 hours. Oxygen and pH were monitored throughout the experiment, oxygen being determined by the Winkler method and pH being continuously recorded with a Leeds and Northrup pH meter.

In another experiment, India ink was used to simulate the permeator or substance diffusing from the medium into the plant cells. Individual particles could be counted under the oil immersion lens of a compound microscope. Although the size range of India ink particles was at the upper limit and above the size range of colloidal suspensions, the behavior of the particles was useful for analogy. Molecules and ions in solution are subjected to stronger intra-molecular forces than suspended particles, hence their behavior should resemble but not perform precisely as ink particles.

The water in a circular tub was rotated by a jet of air from a compressor. The air was warmed to decrease temperature variations as the speed of the jet was increased. An aliquot of India ink was introduced into the tub of swirling water and allowed to become uniformly dispersed. The flow rate of the water was determined by timing the transit of bits of submerged paper for each run, and the rates normally occurring in lagoon tidal channels were used. Glass slides were prepared by slipping onto them small sections of AA Millipore membrane filter[2]. The filters were cemented to one end of each slide with Haupt's solution. The firmly supported slides were lowered into the swirling water, filter surface toward the flow of the medium, to a depth of 3 cm. and held there for 5 seconds. Care was taken not to immerse the slide into the froth that collected at the outer periphery of the tub.

The slides were then removed and cleared with creosote and counts were made of the ink particles in eight entire microscopic fields at 900X magnification. During all runs the tub water was maintained at 24°C. The increased pressure of water against the fixed slides with increased flow rates was considered to be a realistic variable in the model. The model was intended to simulate the passive transport of substances to cell walls and membranes, but not the diffusion of substances into the cell membrane.

The current velocity component over a given marine habitat has not been quantitatively defined by ecologists as a regime. A system is proposed which evaluates the current regime for a given habitat whether it be in fresh-water or sea water. Hourly measurements of the current velocity, in cm. per second, are made at a given habitat. In tidal waters data are collected during complete neap and spring tidal cycles. The hourly spring and neap measurements are averaged and summed, then graphed, plotting current velocity with time. The area of the graph is then calculated and divided by the time to obtain the average lunar period velocity of the regime expressed in knots.

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[2] Millipore Filter Corp., Bedford, Mass.

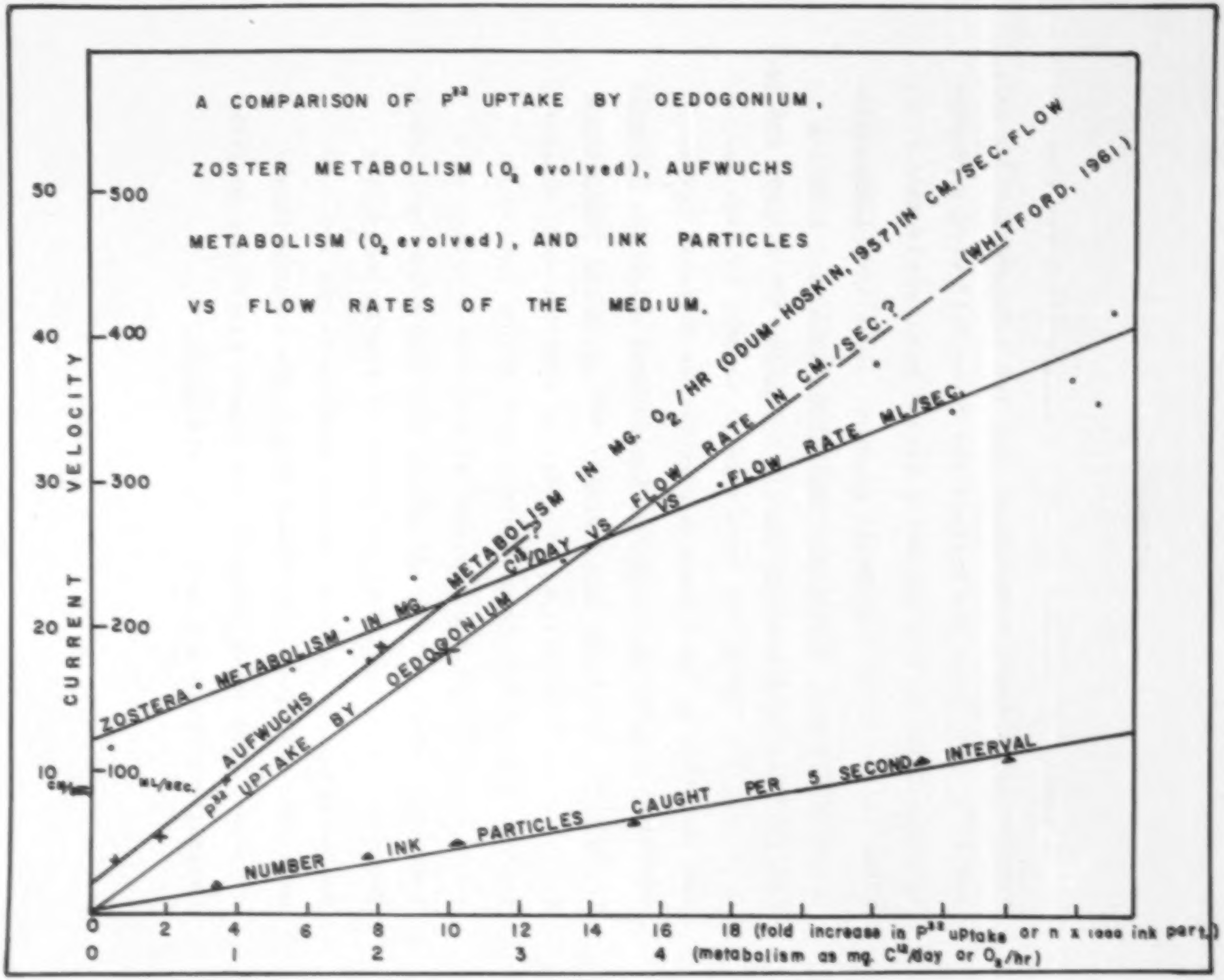
RESULTS

Results from the incubator experiment on Zostera metabolism related to flow rates of sea water (Figure 1; note data for Zostera) show gross and net production rates which could be raised or lowered by changing the recirculation velocity of the sea water. These data support earlier work indicating that more rapidly moving water is related to increases in metabolic rates in some plants. Odum and Hoskin (1957) witnessed the same phenomenon for a blue-green algal community in their experimental microcosm. Odum and Hoskin (Ibid.), Conover (1958), and Whitford and Schumacher (1961) concur that the connection between current velocity and plant metabolic rates is believed to be a function of the rate of transfer of required gaseous and dissolved nutrients from the water into the organism.

Standing crop data for Zostera communities growing in Charlestown Pond, Rhode Island were selected from studies conducted there in May 1963. These data were taken from a number of habitats each representing different current velocity regimes (see methods and Figure 1). The data are shown in Figure 2. These data for the growth of Zostera agree favorably with the laboratory results.

FIGURE 1

Results from Zostera metabolism experiments in the author's incubator studies, data from Odum and Hoskin (1957), from Whitford's studies..extrapolated (1961) and the writer's India ink experiment related to current flow. These data show a strong correlation exists between assimilation, metabolism, transport catchment (particle presentation at a tissue surface) and the movement of the medium.



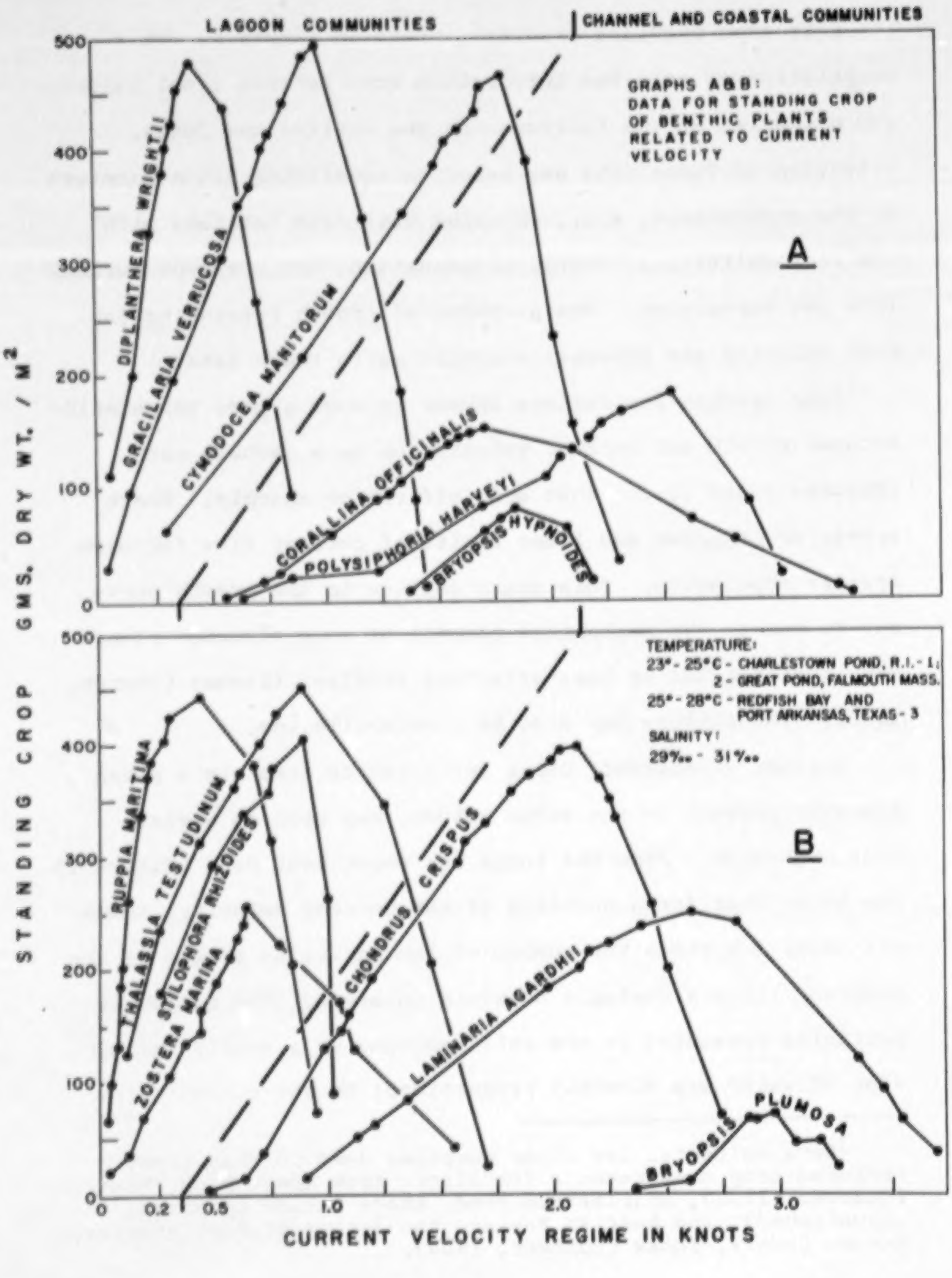
A COMPARISON OF P^{32} UPTAKE BY OEDOGONIUM, ZOSTER METABOLISM (O_2 evolved), AUFWUCHS METABOLISM (O_2 evolved), AND INK PARTICLES VS FLOW RATES OF THE MEDIUM.

5-5c.

FIGURE 2

A family of seasonal growth curves are given for some benthic plant taxon communities from two latitudes, 41°N. Lat. and 28°N. Lat. from New England and Texas Gulf waters respectively. Data for the following taxons from Charlestown Pond, Rhode Island include *Bryopsis plumosa*, *Corallina officinalis*, *Chondrus crispus*, *Gracilaria verrucosa*, *Laminaria agardhii* *Polysiphonia novi-angliae*, *Ruppia maritima*, and *Zostera marina*. Other species listed are from a Texas lagoon, Redfish Bay, and the jetty at Port Aransas near Corpus Christi, Texas, including *Cymodocea manitorum*, *Diplanthera wrightii*, *Bryopsis hyponoides*, *Corallina officinalis*, and *Thalassia testudinum*.

Note that the cluster of plots of standing crop against current regime tend to separate lagoon plants into quiet water habitats and open coastal plants into swifter, more turbulent water. Other parameters are also causally related. The more gradual drop-off in growth of plants beyond the curve vertex in the open coastal plant data may indicate metabolic failures since these plants are usually firmly attached. The sharp drop-off for lagoon plants may be both metabolic failure and mechanical attrition.


LAGOON COMMUNITIES
CHANNEL AND COASTAL COMMUNITIES
GRAPHS A&B:
DATA FOR STANDING CROP
OF BENTHIC PLANTS
RELATED TO CURRENT
VELOCITY
A
DIPLANTHERA WRIGHTII
GRACILARIA VERRUCOSA
CYMODOCEA MANITORUM
CORALLINA OFFICINALIS
POLYSIPHORIA HARVEYI
BRYOPSIS HYPNOIDES
TEMPERATURE:
23° - 25°C - CHARLESTOWN POND, R.I. - 1;
2 - GREAT POND, FALMOUTH MASS.
25° - 28°C - REDFISH BAY AND
PORT ARKANSAS, TEXAS - 3
SALINITY:
29‰ - 31‰
B
RUPPIA MARITIMA
THALASSIA TESTUDINUM
STILOPHORA RHIZOIDES
ZOSTERA MARINA
CHONDRUS CRISPUS
LAMINARIA AGARDHII
BRYOPSIS PLUMOSA
STANDING CROP GMS. DRY WT. / M^2
500
400
300
200
100
0
0
0.2
0.5
1.0
2.0
3.0
CURRENT VELOCITY REGIME IN KNOTS

Data from previous studies[3], given in Figure 2, are a compilation of selected information from several tidal lagoons and estuaries at two latitudes in New England and Texas. Selection of these data was based on equalizing all parameters of the environment, e.g., choosing data from habitats with the same salinities, depth, illumination, etc., except current flow and turbulence. The patterns of growth related to current velocity are strongly established in these data.

Some species populations appear to show a good correlation between growth and current velocity up to a certain rate (Figures 2 and 3) and then drop off rather sharply. There appear to be upper and lower limits of current flow for each species population. This sharp decline in the growth curve may be due to the mechanical removal of some attached plants with poor ballast or less effective holdfast tissues (Church, 1909). The failure may also be a metabolic one.

Another experiment, using India ink to simulate a given property present in the water column, may help to explain this mechanism. From the India ink experiment data (Figure 1) one notes that for a doubling of the current velocity, there was about 3.6 times the number of ink particles caught on the membrane filters during a 5 second interval. The number of particles presented to the cell membrane in a nearly laminar flow of water was directly proportional to the current flow

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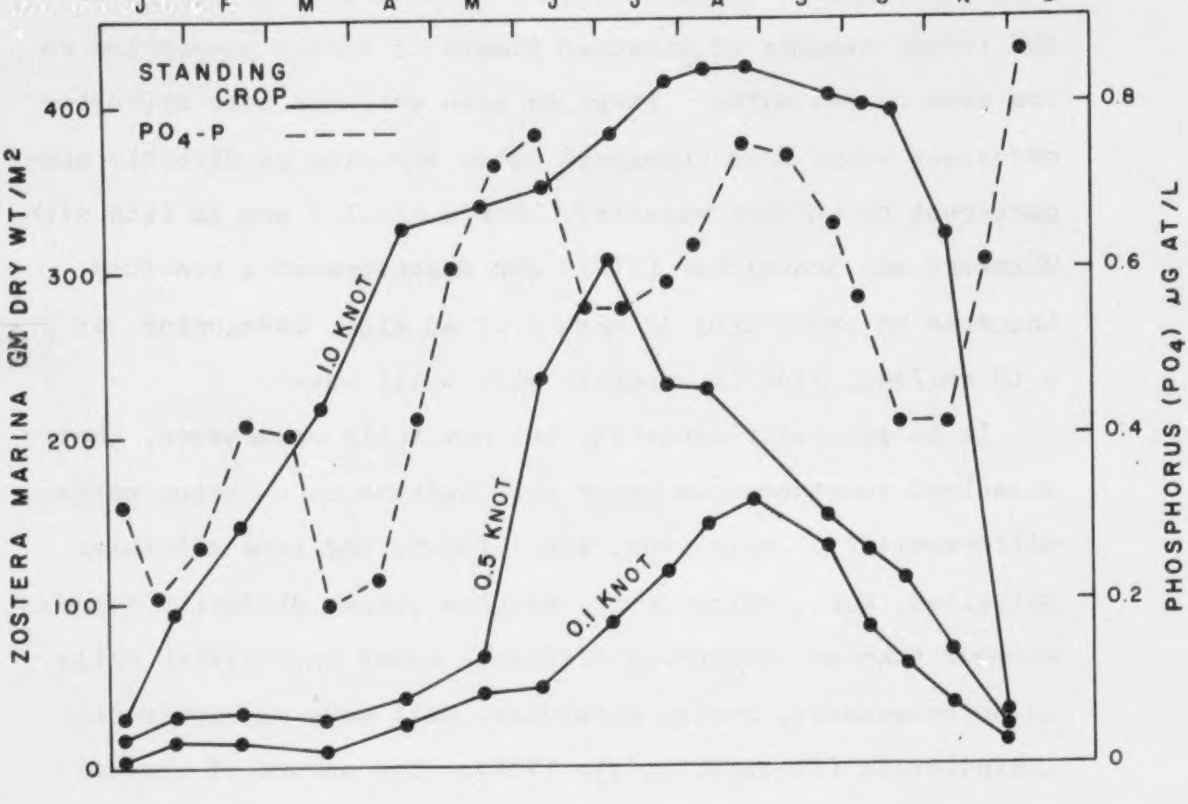
[3] Data collected for other purposes used in this study included crop measurements for plants from Great Pond, Mass. (Conover, 1958), Charlestown Pond, Rhode Island (Conover, unpublished), and Redfish Bay and the jettys at Port Aransas, Nueces County, Texas (Conover, 1964).

FIGURE 3

Three growth curves are given for Zostera marina from Charlestown Pond, Rhode Island, 1962-63, relating seasonal growth with current velocity regimes. Note the higher the current, the more rapid the growth as related to the PO_4-P pulses. All three habitats were selected with seasonal inorganic phosphate data in near agreement. The writer postulates that the assimilation rates do differ in these three communities. Zostera growing in slower current regimes tends to show greater growth later in time, possibly related to the largest phosphate pulse in the system. The growth trends shown suggest that transport and diffusion are playing a major role in the seasonal metabolism and growth of these plant communities.

5-64



J
F
M
A
M
J
J
A
S
O
N
D
STANDING CROP
PO4-P
1.0 KNOT
0.5 KNOT
0.1 KNOT
ZOSTERA MARINA GM DRY WT/M2
0
100
200
300
400
PHOSPHORUS (PO4) µG AT/L
0
0.2
0.4
0.6
0.8

of the medium. With the introduction of turbulence diffusion processes are generally increased. An increase was noted in ink particles caught on the filters when turbulence was permitted to develop in the tub.

The inferences drawn from these two laboratory experiments and the selected field data from natural communities are that substances dissolved in water are mechanically presented to the living tissues of attached plants in direct proportion to the flow of sea water. There is also evidence that diffusion processes related to transport rates may also be directly proportional to current velocity. These results are in line with Whitford and Schumacher (1961) who demonstrated a ten-fold increase in phosphorus 32 uptake of an alga, Oedogonium, in a 18 cm./sec. flow in contrast with still water.

It is generally accepted, but not fully understood, that dissolved substances in water will diffuse into living cells differentially. Most ions, e.g., PO_4-P, and some molecular solutions, e.g., amino acids, require active diffusion forces to move them at reasonable diffusion rates into living cells. Other substances, mostly molecular, will move passively into living cells (Steward, et al, 1959). The nature of the cell membranes themselves is usually involved. Some membranes offer more or less resistance to diffusion processes due to the requirements of the permeators which must dissolve first from water into the membrane and then return to an aqueous phase within the cell (Ibid.). Quite apart from these complex relationships ultimately all diffusion processes, active or passive, must depend upon the mechanical presentation of substances in contact with the cell membrane at the sea water-membrane interface.

Why do some plant species grow optimally in stagnant or slow-moving water while others require more rapid flow rates? The key to these distinct differences may be genetically controlled for certain metabolic rates inherent for each species. A function of metabolic rates are the assimilation rates (Steward, _et al_, 1959). If the concentrations of substances normally absorbed are presented to the sea water-cell membrane interface in direct proportion to the current velocity, there should be a correlation between metabolism rates and growth rates as a causal avalanche. Field data (Figures 1 and 4) support this view. The data in Figure 4 would strongly suggest that plants may absorb a phosphate ion more readily in more rapidly moving water.

If a plant has a naturally high metabolic rate, genetically controlled, the uptake rate of required raw materials should be higher than that for plants with lower metabolic rates. This relationship has not been demonstrated for various benthic marine plants but differences in metabolic rates and assimilation rates for terrestrial plants is common knowledge (_Ibid_.). The concept of genetically controlled sensitivity of certain species to grow best in certain moving water regimes is speculation at this point. But there is evidence (Gessner, 1955) that some benthic plants will use up additional energy for active assimilation processes to compensate for low concentrations of required substances in the medium. The compensatory metabolic rate increase above normal for benthic marine plants growing in brackish water habitats has been reported by Gessner (1955). Hence, plants which must increase their metabolic rate under physiological stress may attain a growth "compensation point" due to assimilation failures rather than the usual one associated with minimal illumination.

Up to this point in the discussion we have been concerned with compensation for low concentrations of required substances. Let us consider now the role of current velocity with respect to substances occurring in excessive concentrations. Experimental studies with root tissues of terrestrial plants have shown that excess concentrations of some ions or molecules at the soil-water/root hair cell membrane interface tend to inhibit the diffusion of other ions or molecules of other substances entering or leaving the cell (Steward, et al, 1959). With an increase in the flow of water over an aquatic community it is conceivable that the postulated higher concentrations of excess ions or molecules of some substances could hinder the diffusion of other substances. The shortage of some required substances by this process could limit growth.

This hypothesis, if valid, would require a complete reevaluation of nutrient cycle estimates for benthic and perhaps planktonic plant community metabolism. Calculations of phosphorus and nitrogen budgets in a body of water may require an adjustment for current velocities to obtain more realistic estimates. Using this experimental approach on data from a Rhode Island estuary, the writer has obtained good correlations (in this report) between benthic plant production and flowing water in contrast to still water by adjusting the nutrient data to the current regime of the habitat.

If these principles apply to assimilated substances, why should they not also apply to exuded metabolites? Some exogenous metabolites from benthic algae are known to have strong antibiotic as well as probiotic properties (Conover with Sieburth, 1964; Sieburth with Conover, 1965). The antifouling of some algae, free of epibiota which results from the presence of certain metabolites (e.g., tannic acid) during the growth season, may be strongly influenced by the current velocity of the medium. Data on hand tend to support this view.

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THE IMPORTANCE OF STEM AND LEAF *VS*. ROOT ASSIMILATION IN *RUPPIA MARITIMA* L. AND *ZOSTERA MARINA* L. RELATED TO SEASONAL GROWTH

by

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INTRODUCTION

In the truly immergent aquatic plants including Zostera marina, Ruppia maritima, and Potomogeton species, assimilation of gases and mineral nutrients required for metabolism is believed to take place in roots, stem, petiole, and leaf organs. Earlier workers made this assumption on anatomical and autecological evidence (Constantin, 1886; Sauvageau, 1891; Hill, 1908; Dittmer, 1949; and Pond, in Gessner, 1955). Sauvageau reported a lack of stomata in the leaves, a great reduction of vascular tissue, especially xylem, a minimum of supporting tissue and cuticular development of the epidermis and the development of very thin-walled cells in all tissues. The functional root system he described as developing adventitiously, the primary root being lost early in development. The secondary, or adventitious root system, he reported, was greatly reduced; hence, he assigned to it a minor role in assimilation in contrast to that of stem and leaf.

Some experimental work was done by Wilson (1936), Cormack (1937), and Dittmer (Ibid.) on root hair development in aquatic plants which indicated that growth of the hairs was repressed by illumination, suggesting that photosensitive hormones were involved. Pond (Ibid.) undertook experiments with both immergent and emergent plants including Potomogeton, a close relative of Ruppia, to determine the assimilation role of roots vs. leaves in some aquatic fresh-water plants. He reported correlation between good growth of the plants and mineral-rich soils. These early experiments were limited because the absorption efficiency and surface areas of leaf vs. root were not considered and the physical and chemical nature of the soil environment was not analyzed. Another oversight was the role played by the seasonal or life history of the plants related to assimilation processes.

Brown (1913), working with Elodea (=Anacharis), drew attention to the "thin-skinned" anatomy of hydrophytes, e.g., thin cuticles, minimal supporting tissue, thin cell walls, attenuated leaf and stem structures, as reflecting an adaptation to the aquatic habitat. He suggested that these plants evolved their unique anatomical structure for the more rapid passage of gases and dissolved required substances from the water. Further, he stated that some plants overcame the limitations of slow water movement by developing large absorption surface areas. The diffusion of oxygen into aquatic plant tissues, he stated, should be more critical than that in land plants since there was far less oxygen by volume in water than in the atmosphere. Intercellular lacunae, therefore, probably played an important role in storing excess oxygen liberated in photosynthesis for use in respiration where free oxygen was limited or absent in the sedimentary environment. This hypothesis was based upon Van Tieghem's (1866) discovery of nearly pure molecular oxygen trapped in some aquatic plant tissues. In support of his theory, Brown pointed out that plants growing in swiftly flowing waters are without intercellular lacunae, whereas those normally associated with quiet waters have well developed lacunae.

Arber (1926) observed that a drastic reduction in current over a fluvial community of Podostemaceae species resulted in the death of the plants. She ascribed the elongated petioles in many emergents to an adaptation for obtaining oxygen in oxygen-poor water-soil habitats. Brown (1913) claimed that the assimilation of CO_2 by the roots was perhaps the most important role these organs played in metabolism. He stressed that hydrophytes are generally most abundant in CO_2 saturated waters. It is well known that CO_2 limiting is common for terrestrial plants as well as aquatics.

This historical background leads us to a reconsideration of the importance of the pathways of assimilation in aquatics in an effort to evaluate the role of seasonal growth and distribution of immergents including Zostera and Ruppia in tidal lagoons. Without this knowledge an interpretation of plant growth related to nutrients, dissolved gases and other parameters of the sediment-water mass environment is nearly impossible. With this end in mind the present study was undertaken.

METHODS

Whole plants of Zostera and Ruppia were collected randomly from each of six different communities. The sand and silt was retained intact around the rhizomes and root structures during transport to the laboratory. The material was carefully washed in sea water in the laboratory and kept in the fresh living state in incubators. Root *vs*. stem assimilation areas were measured by direct morphometry on the living material. A correction factor for the area of root hairs per root surface area based on length and root diameter measurements was established. One correction factor for root area was found applicable for each species, for all seasons, and all environments. Root hair growth patterns are apparently genetically controlled and develop independent of environmental variations. When epiphytes cloaked the petioles and leaves of plants, a correction for the average area covered was taken into account and subtracted from the absolute area of the stem, petiole, and leaf area of each plant.

Roots, rhizomes, stem, petiole, and leaf tissue were fixed in Crafts chrome acidic acid, schedule III, embedded in paraffin and sectioned, then studied under a phase contrast microscope. Camera lucid drawings and polaroid microphotographs were taken from the fixed material.

To test the rapidity with which a vital dye, congo red, was absorbed by leaf and root tissues _in vivo_, plants were immersed for 5 minutes in moderately stained sea water. The plants were removed and frozen sections were made and studied to determine how widespread the dye had penetrated the tissues of the various organs in a given length of time.

RESULTS

Do natural populations of Zostera and Ruppia rooted in nutrient-rich sediments grow better than those rooted in nutrient-poor sediments? The most luxurious plant beds of these two immergent species grow in areas of the lagoon where the sediments may be either nutrient-rich or poor (Figure 1[1]). Apparently the nutrient content of the sediments was not solely responsible for the growth patterns of the sea grasses (Figure 2[1]). If growth is used as the criterion, these results suggest that Zostera and Ruppia have no clearcut dependency on sediments for nutrients.

Some of the highest gross production and standing crop measurements for plant communities in Charlestown Pond are maximum on sandy, shell-strewn bars or in silt-laden basins in the tidal current tracks of the lagoon (standing crop of 100 g. to 200 g. dry wt./M^2 and from 0.5 to 1.5 g./M^2 carbon fixed per day, gross production). A study of the role of moving waters and their effect upon natural diffusion gradients (Conover, in this report) indicates that moving waters are directly related to higher assimilation rates in attached plants. The counterpart of these observations is the presence of lower gross and standing crop values for plant communities occupying quiet, back-water slough areas where exchange is minimal (note data, Figure 2). Since this picture is not always consistent, other factors must be involved in some habitats.

The correlation between growth and the presence of gaseous as well as dissolved nutrients in the water column is unmistakable in these data (Figure 4). If the root systems are absorbing some of the nutrients, the effect this source has on growth appears to be masked by processes taking place in the upper portions of the plants.

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[1] Figures 1 and 2, see Appendix figures A-18 and A-24, respectively.

Is the greatly reduced root system in both species ineffective as an organ of absorption? To evaluate the role of the root system as an efficient assimilatory organ, the root anatomy of both species was studied. A detailed anatomical examination of the roots of these plants shows that the roots and root hairs are highly specialized to provide a maximum surface area for assimilation considering the size and area of the root system exposed in the sediments (Figure 3). As few as six roots and as many as thirty, each 1 to 6 cm. in length, develop from each rhizome node in Zostera. From two to twelve rhizome nodes may be present, the most distal dying out as new nodes replace the old. In Ruppia there may be as few as three and as many as twenty with two to fifteen rhizome nodes present.

There is good anatomical evidence from plasmolytic and puncture experiments on both species that these roots and root hairs are viable and are probably active in assimilation processes. Note in Figure 3 that the root hairs are persistent all the way to the base of the root in both species. These root hairs heavily cloak the short 2 to 5 centimeter-long roots despite the variability of the sedimentary environment.

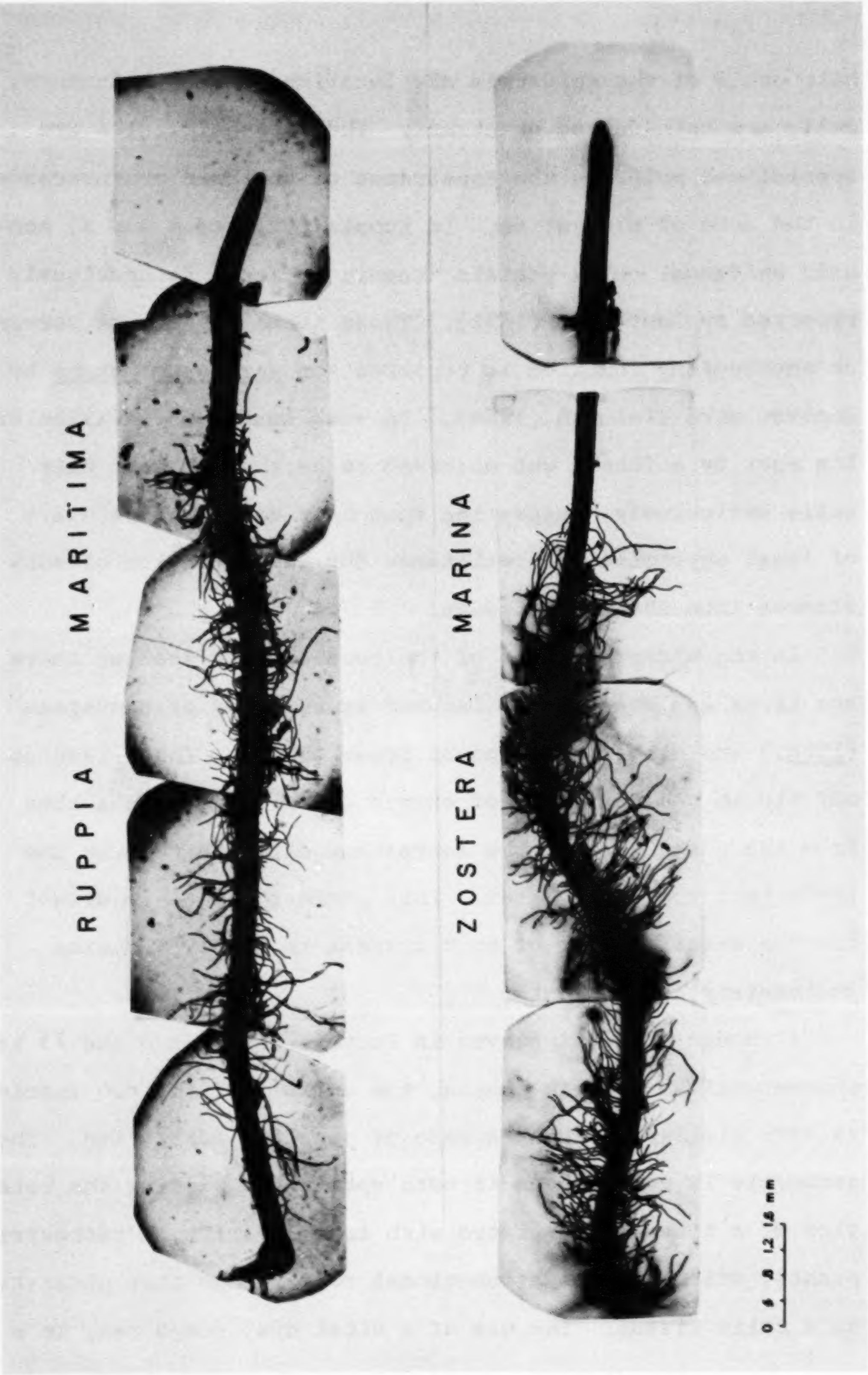
In the root of both species the vascular stele is small and there are mostly phloem elements present. Rarely does one find xylem elements in the vascular strand. A conspicuous pericycle develops in both species. A collenchyma appears in the roots of both species just below the epidermis. Often the

6-7a

FIGURE 3

Untouched photographs of whole roots showing the extensive root hair zones.

6-7b



hair cells of the epidermis are localized where collenchyma cells are thin-walled or absent. The root hair cells are specialized prior to the appearance of the hair protuberance in the zone of elongation. In Ruppia (Figures 4 and 5) non-hair epidermal cells contain "tannin bodies", as previously reported by Sauvageau (1891). These "tannins" may be serving an antifouling function as reported for Sargassum natans by Conover with Sieburth (1964). In some instances invasion of the root by a fungus was observed to be through root hair cells exclusively, suggesting that hair cells are pathways of least physiological resistance for the diffusion of substances into the root tissues.

In the older portions of the root of both species there are large gas chambers or lacunae as reported by Sauvageau (Ibid.) and elaborated upon by Brown (1913). These lacunae may aid in the diffusion of oxygen which has been absorbed from the water through the leaves and diffused through the stele into the root system. This process may be important for the establishment of root systems in highly reducing sedimentary environments.

Although the collenchyma in Zostera (Figures 6 and 7) is thinner-walled than in Ruppia, the anatomy of the two species is very similar, arguing a case of parallel adaptation. The pericycle is conspicuous in both species suggesting the retention of a tissue, associated with translocation in terrestrial plants, which retains a functional role rather than persisting as a relic tissue. The use of a vital dye, congo red, in a

FIGURE 4

Ruppia maritima, longitudinal sections from root cap to root base. Note indicator letters which represent the intersects of the cross sections shown in Figure 5.

6-8b

RUPPIA MARITIMA

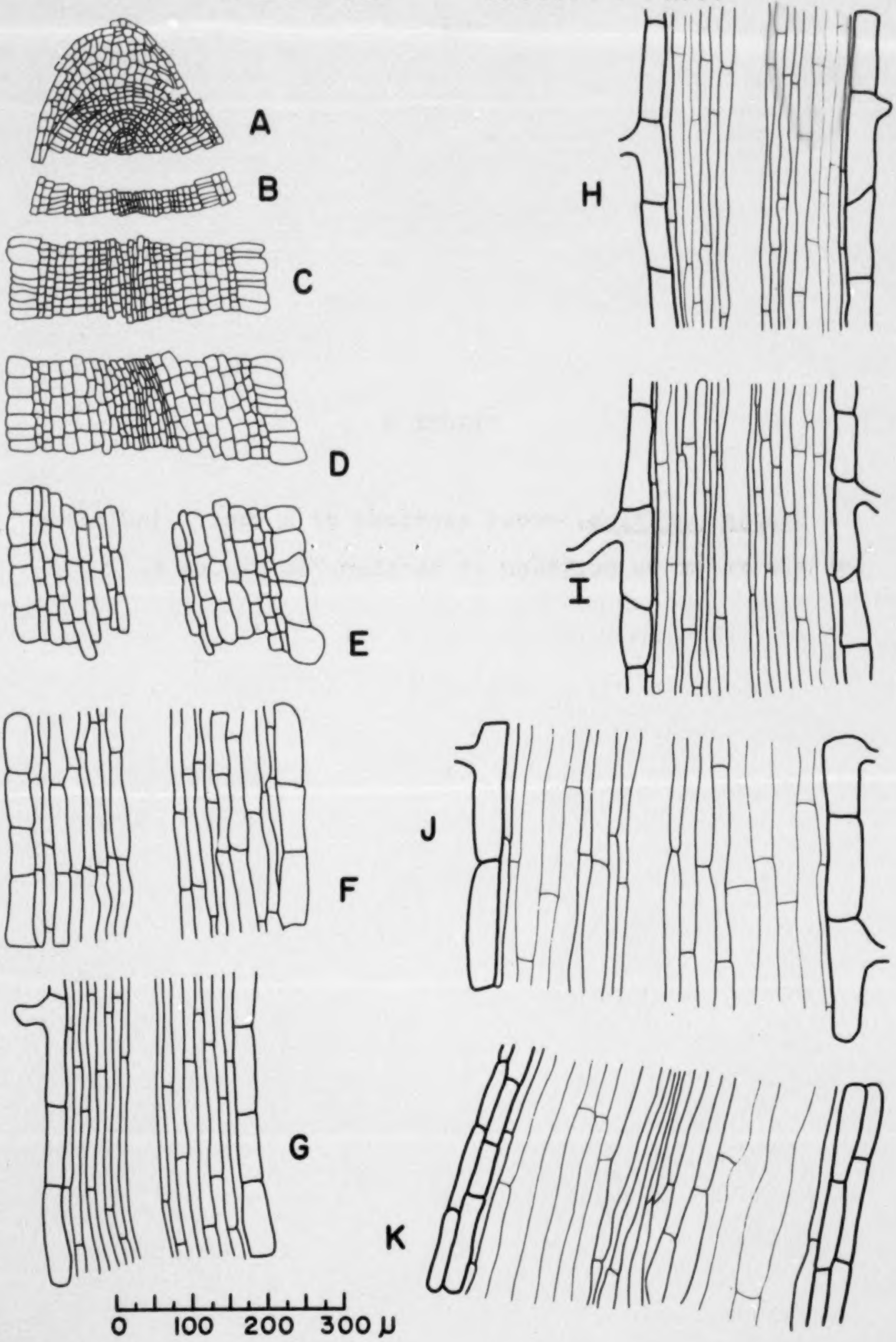


FIGURE 5

Ruppia maritima, cross sections of a root. Indicator letters refer to position of sections in Figure 4.

6-8d

RUPPIA MARITIMA

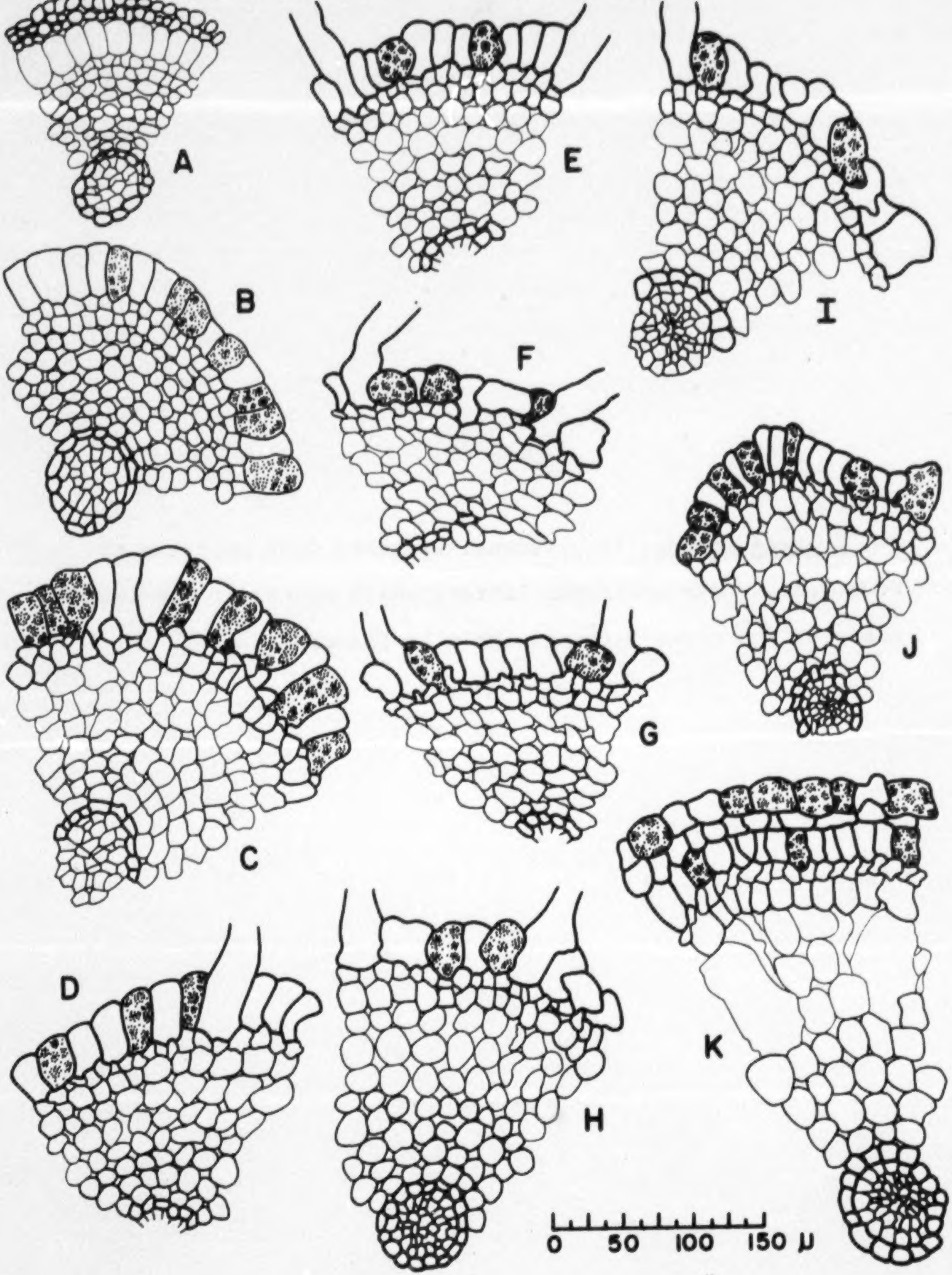


FIGURE 6

Zostera marina, longitudinal sections from root cap to root base. Note indicator letters which represent the intersects of the cross sections shown in Figure 7.

6-8f

ZOSTERA MARINA

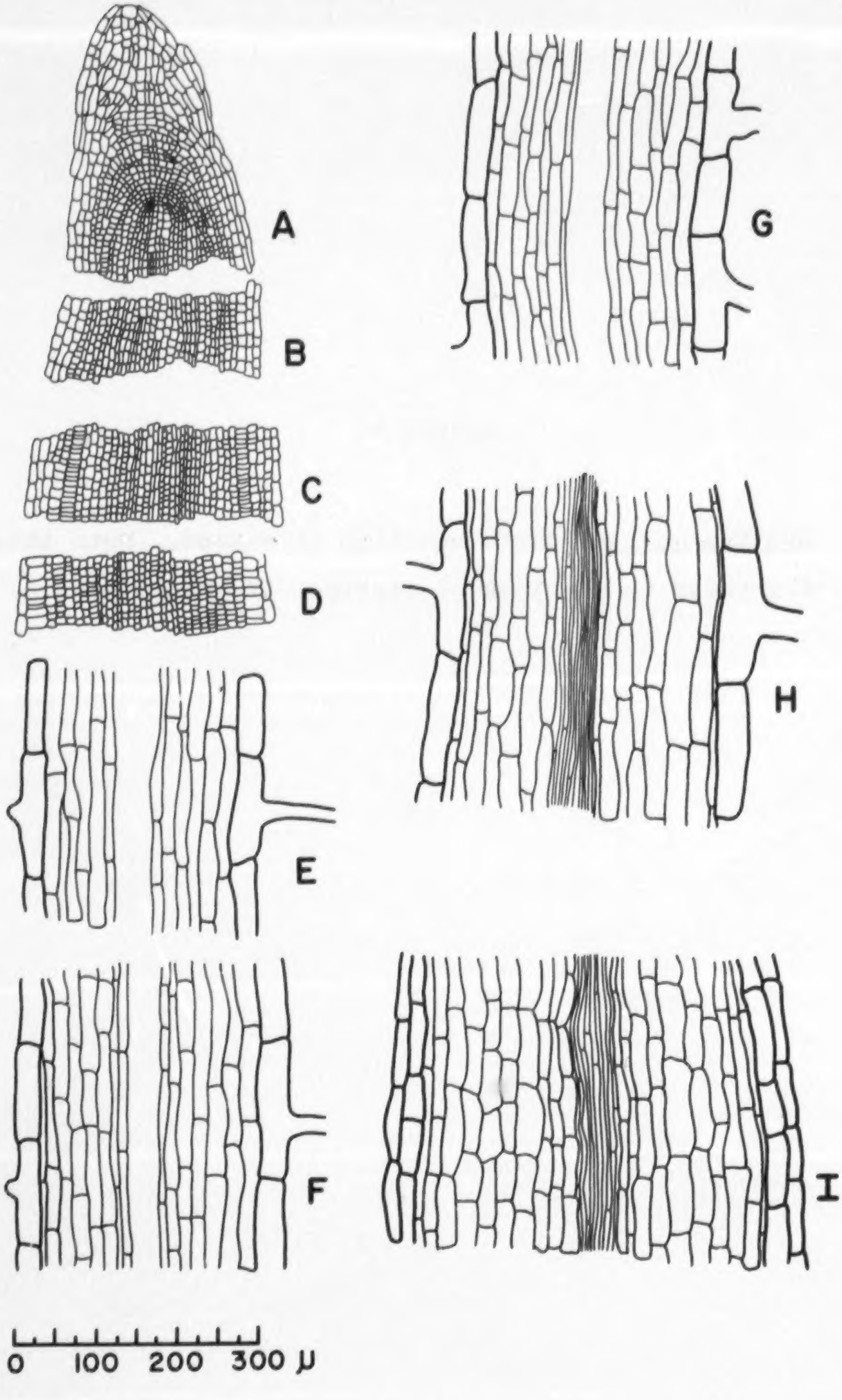
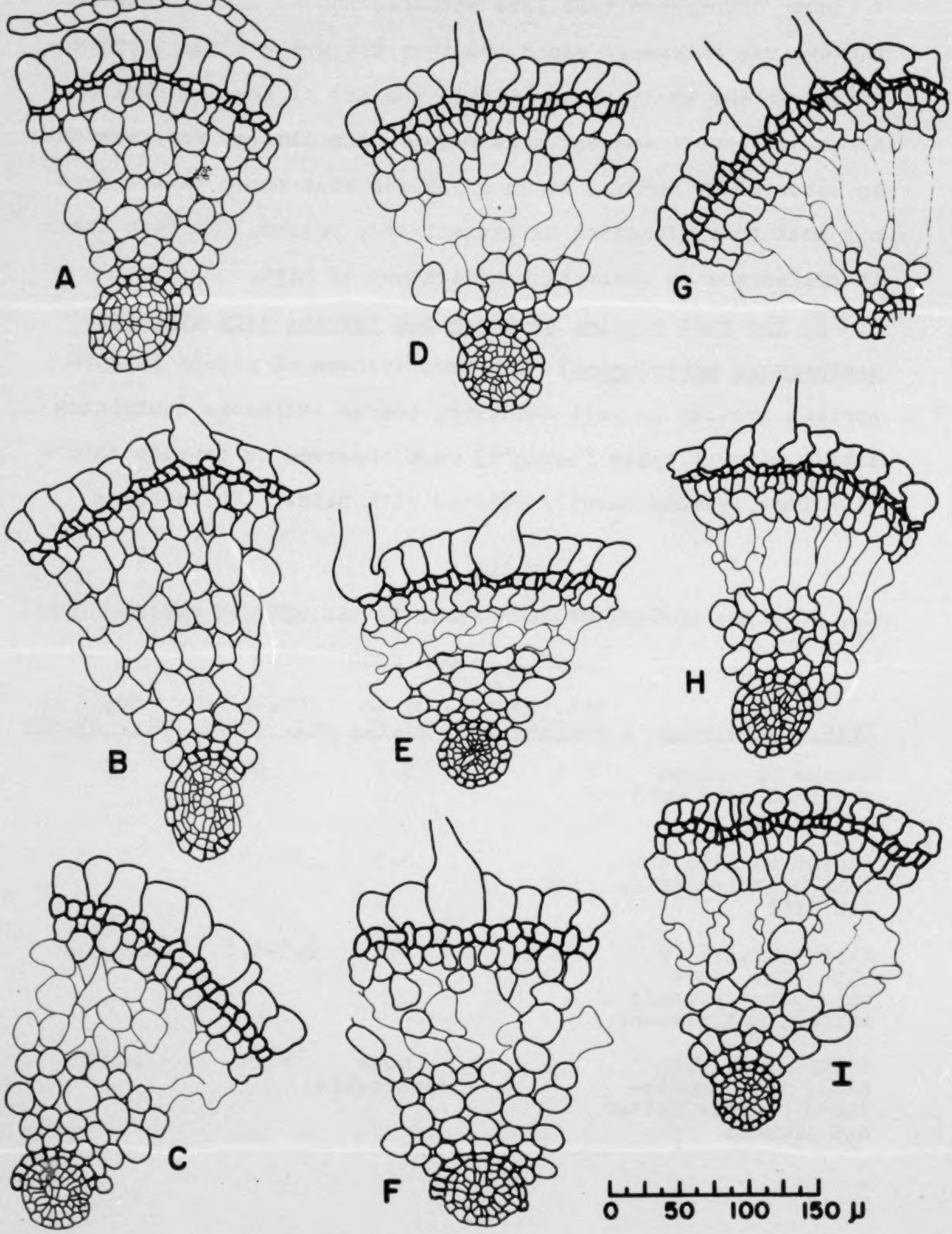


FIGURE 7

Zostera marina, cross sections of a root. Note indicator letters refer to position of sections in Figure 6.

6-8h

ZOSTERA MARINA



5 minute absorption test (see methods) showed that uptake of the dye was extremely rapid and that the dye was found concentrated in the stele tissue within the arc of the pericycle. These data would suggest that despite the limited root systems in Zostera and Ruppia, it would appear that these organs have not lost their function as assimilatory organs. In fact there is evidence that absorption efficiency is high.

Do the root systems of these two species vary with the sedimentary environment? The root systems of plants in both species growing in well oxidized, coarse sediments containing little mineral salts (Table 1) were observed to develop extensive root systems heavily cloaked with hairs. In Japanese

TABLE 1

O_2, PO_4, NO_3 CONTENT OF FOUR TYPES OF SEDIMENTARY ENVIRONMENTS IN CHARLESTOWN POND

Type of Sediment	Ref. type (see Fig. 9)	O_2 in ml./L.	PO_4-P in µg. at./L.	NO_3-N in µg. at./L.
Coarse to medium oxidized sand with pebble and shell	D	5-7	.01	.05
Medium to fine sand, some organic matter and silt	C	3-5	.08-.3	.1-.5
Fine sand, silty with clay, some unoxidized organic matter, H_2S present	B	1-2	2.4-4.5	2.0-6.5
Silty sand, with clay, much unoxiddized organic matter H_2S present	A	none detectable	>100	>250

waters, Moritoshi (1950) observed no establishment of *Z. marina* in sandy and pebble-strewn sediments, but found them growing only in sandy-silts and mud. In New England waters, plants that develop the most elaborate root systems of any in the lagoons are those growing in the coarse sandy sediments. Quite often the roots of these plants are found washed clear of the sediment and exposed to the water. A similar situation obtains with *Thalassia testudinum* in similar habitats along the Texas Gulf Coast and in Biscayne Bay, Miami, Florida.

It is suspected from measurements of molecular oxygen in these coarse sediments that the enhanced root growth may be related to the high partial pressure of oxygen together with the relatively low concentration of ions, molecular metabolites, and gases. By contrast those plants growing in fine-grained, rich organic oozes, which contain high concentrations of carbon dioxide, hydrogen sulfide, methane, minerals, and metabolites, have poorly developed root systems and limited rhizome development. In very highly reduced sediments the roots of both plants are unable to grow. Only a few nodes of stunted rhizomes survive in Zostera. In Ruppia an extreme is observed in the complete degeneration of the root-rhizome system in some cases leaving only stem, petiole, and leaf organs which continue to grow on the surface of the organic ooze.

By the very physical nature of a tidal estuary where saltwater meets fresh (Rochford, 1952) the sedimentation within the system results in the deposit of organic-rich clayey-silt oozes throughout most of the major basins and sloughs of the lagoon. These basins and sloughs are the habitat for the greater portion of the immergent sea grass populations in Rhode Island lagoons. As a consequence, a knowledge of the relationship between the root systems and the sedimentary environment is extremely pertinent to this discussion. Since oxygen is consumed in respiration to mediate active absorption, the lack of oxygen in the molecular form affects root metabolism. This limitation is serious when roots are growing in oxygen-poor sediments characteristic of reducing environments.

As indicated in Table 1, these organic oozes contain very high concentrations of phosphate, nitrate, and other minerals and metabolites. It is conceivable that these substances are so concentrated that they may inhibit development and absorption processes for normal metabolism and growth of sea grass roots and rhizomes. The minimal development of roots and rhizomes in these muds supports this view (Table 2). In between these two extreme types of sedimentary environments are intermediate conditions. Plants growing along this graded series of sediment types, from oxidizing to reducing environments, possess rhizome and root systems intermediate in development to those described for the extremes.

It was pointed out by Howard Sanders (personal communication) that morphologically stunted and reduced root systems might have little absorption area exposed to the sediment but in the presence of high concentrations of required substances might absorb large quantities per unit area. This point has doubtful validity on the basis of what has been learned about

TABLE 2

ROOT AREA RELATED TO FOUR TYPES OF SEDIMENTARY ENVIRONMENTS

Type of Sediment	Ref. type (see Fig. 9)	Ruppia cm.^{2}/plant	Zostera cm.^{2}/plant
Coarse gravelly sand, oxidized organic matter, O_2 content high, color light gray to brown.	D	14-33	38-56
Medium sand and pebble some unoxidized organic matter, trace H_2S, low O_2, color dark gray.	C	8-23	24-52
Silty fine sand, unoxidized organic matter, some H_2S, color very dark gray.	B	8-16	14-26
Sandy clayey silt abundant organic matter unoxidized, H_2S present, color black.	A	0-11	0-21

soils and their content in relation to terrestrial plant metabolism. The uptake of mineral nutrients, especially phosphate, is recognized as being an active absorption process (Steward, et al, 1959) and requires molecular oxygen. The anatomical evidence for both species of sea grasses points to a minimal area of root absorption for active uptake, as in Ruppia, or a total lack of roots in extreme reducing environments. The correlation is unmistakable, indicating that root growth and development in Zostera and Ruppia is a direct function of the type of sedimentary environment, including clay content, pH and eH, as well as metabolite, mineral, and gaseous content.

Do root absorption areas differ seasonally in Zostera and Ruppia? The root system for a given plant will show little change (Table 3) in its total area seasonally except for slow renewed growth in spring and early summer. As was mentioned above, there are real differences in the area of root systems of plants in different sedimentary environments in a lagoon but area does not vary seasonally.

TABLE 3

ROOT AREA CHANGES RELATED TO SEASONAL GROWTH IN ZOSTERA MARINA L.

Month	Stem-Leaf Area/cm.^{2}	Root hair Area/cm.^{2}	L:R Ratio
Jan.	118	22	5:1
Mar.	142	24	7:1
May	420	28	12:1
July	530	34	15:1
**** PERIOD OF DEHISCENCE ****			
Oct.	43	7.1	6:1
Dec.	138	21	7:1

Is there a seasonal change in the stem and leaf assimilation area in these sea grasses? Seasonally, the stem and leaf of Zostera and Ruppia undergo a regular cycle of growth in the warmer months followed by a late August dehiscence period. In the warmer months many plant and animal organisms form an epibiotic covering on much of the leaf area of both species, thereby reducing the assimilation efficiency of the leaf epidermis. Consequently, the leaf and petiole assimilation area varies widely with the time of year (Table 3) in both Zostera and Ruppia. In Zostera the second year leaf blades are shed, whereas many first year blades are retained. Zostera grows all the year in Rhode Island waters while Ruppia is dormant in the coldest months (Conover, 1965).

Do the stem, petiole and leaf assimilation surfaces vary in area from one habitat to another? Results (Figure 8) show that for Zostera, and also for Ruppia plants growing in the same sandy sedimentary environment, there are growth increases in those plants which are exposed to more rapidly moving water (Ibid.). These plants are believed to receive more ions or molecules per unit of time.

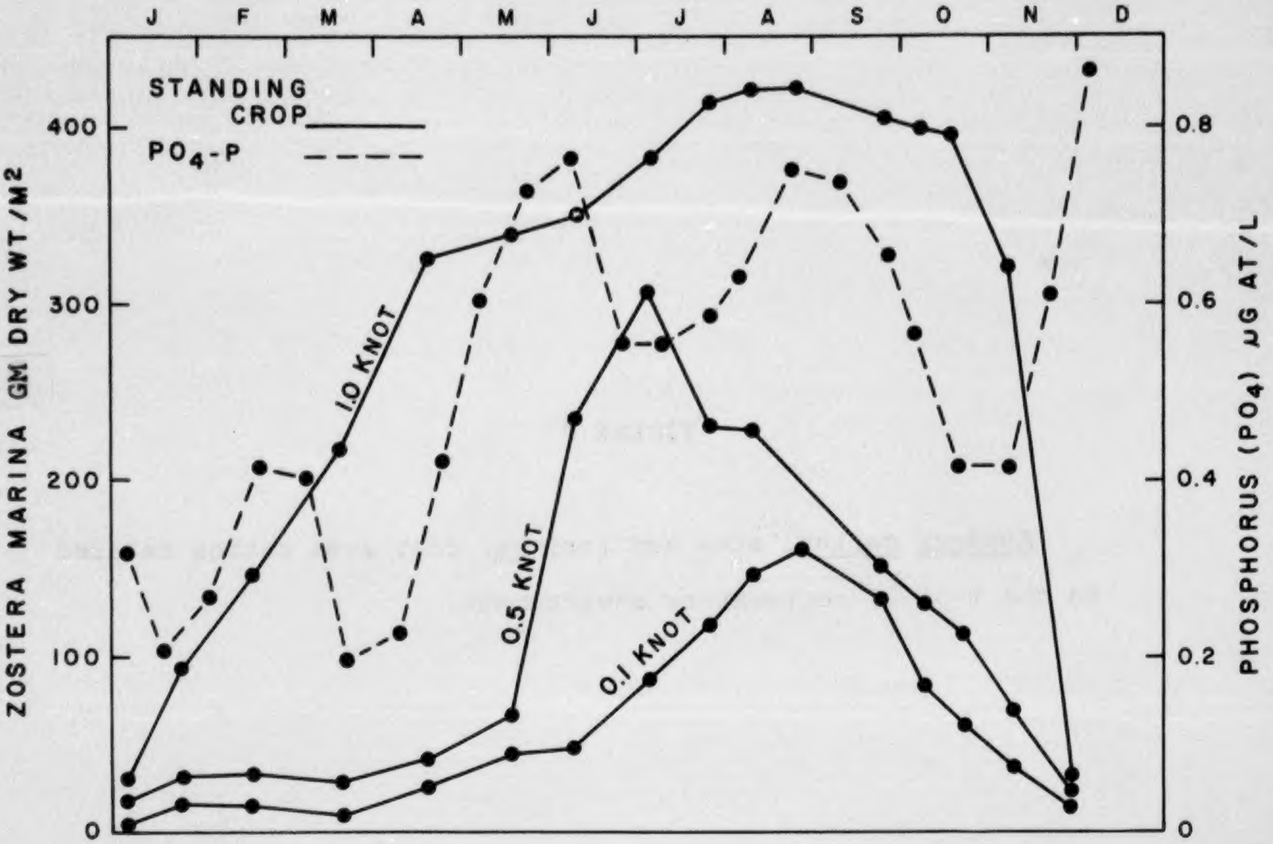
What can be deduced from absorption area root vs. leaf area ratios? To evaluate the role of root systems vs. the leafy portions of Zostera and Ruppia, the ratios of the fraction of the plants in the water column vs. the fraction in the sediments were obtained for plants growing in the four representative habitats in Charlestown Pond, Rhode Island. The results are shown in Figure 9.

Plants used in this study were collected in October when the old blades had dehisced and new blades were developing. There was little difference in blade length between plants growing in various habitats this particular season of the year. Depending upon the habitat, however, more rapid growth appears in some plants than in others as the growing season

FIGURE 8

The effect of currents on nutrient uptake by Zostera marina on de facto evidence from a field study.

6-14b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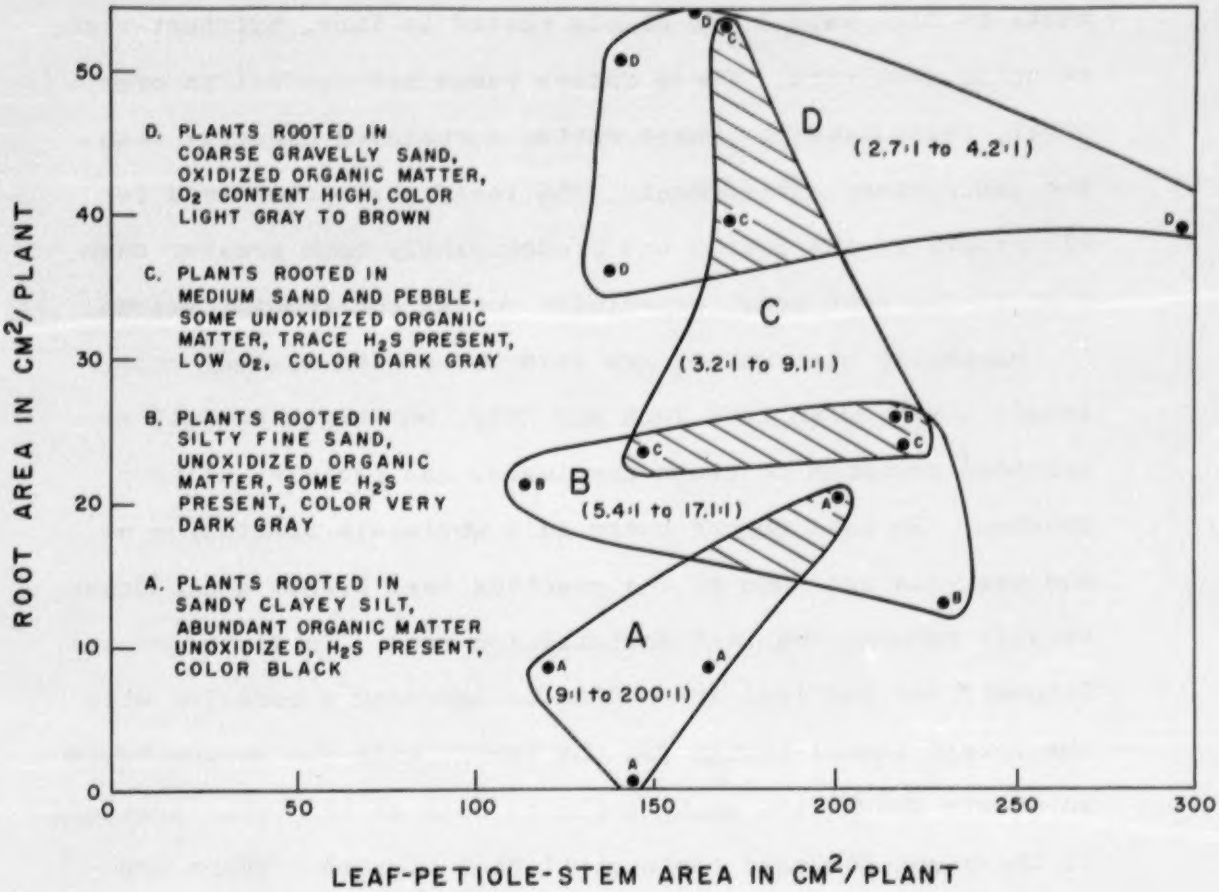
PHOSPHORUS (PO4) µG AT/L
1.0 KNOT
0.5 KNOT
0.1 KNOT
0
100
200
300
400
0
0.2
0.4
0.6
0.8

FIGURE 9

Zostera marina, stem and leaf *vs*. root area ratios related to the type of sedimentary environment.

6-14d

LEAF STEM VS. ROOT RATIOS IN *ZOSTERA MARINA* RELATED TO SEDIMENTS



progresses. The ratios tend to swing from low values for plants growing in coarse, nutrient-poor, well oxidized sediments to high values for plants rooted in fine, nutrient-rich, reducing sediments. These ratios range between 4:1 to over 200:1, respectively. These ratios correlated directly with the sedimentary environment. The leafy absorption area for all plants in the lagoon was predominantly much greater than that of the root area, especially during the growing season.

Maximally high ratios are associated with maximum crop levels attained in late June and July, but begin to fall as epibiota commence to cloak the leaves and petioles of both species. In late August there is a wholesale abscission of the year-old and some of the yearling leaf blades which drastically reduces the leaf assimilation area. In September and October root and leaf areas tend to approach a parallel with the lowest annual ratios for the year. With the spring burst in growth the ratios again begin to soar as the upper portions of the plant dominate the assimilation picture. There are seasonal changes in the ratios for any given plant community within each habitat (Table 3). These ratio changes are related to the life history of the plants.

In habitats where the hydrological properties are optimum for plant growth (PO_4-P in excess of .016 μg. at. P/L.) but sediments are composed of well oxidized, coarse sands and gravels, have a low organic content, and are nutrient-poor and well oxygenated (less than 0.05 μg. at. P/L.), the ratios are characteristically lower. These plants have well developed root systems, long rhizomes, and an abundance of long leaf blades. Plants exhibiting these lower ratios still may obtain a large share of nutrients from the water column. These plants occupy habitats second in importance in the lagoon and may comprise as much as 20 per cent of the area.

The highest ratios are found in plants growing in hydrologically enriched sea water, often in flowing water regimes but rooted in highly reducing environments of fine-grained, organic-rich sediments lacking free oxygen. The root systems are stunted and rhizomes comprise very few nodes. Concentrations of nutrient salts in the sediment often exceed 100 μg. at./L. including phosphate and nitrate ions; these concentrations are above the levels known to be inhibitory to the growth of terrestrial plants.

CONCLUSION

From the evidence presented, Zostera and Ruppia are believed to be more dependent upon hydrological than edaphic properties of the environment. The root systems doubtless do contribute their part to the assimilation of required substances from the sediments but on the basis of surface area and the anatomical structure of Zostera and Ruppia as reviewed in this study, there seems to be little doubt left about the secondary role the roots play in assimilation.

The authors are assuming that the computations relative to the nutrient budgets in a lagoon or embayment and the growth of sea grasses can be evaluated using nutrient data from the water column alone. These observations argue favorably for the importance of the water column as the principle source of nutrients for natural populations of Zostera and Ruppia during most of the growing season. However, uptake by the root system may be an important secondary source when leaf assimilation is minimal in the fall and early winter.

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BENTHIC PLANT COMPOSITION, SEASONAL DISTRIBUTION, PRIMARY PRODUCTION AND ECOLOGY IN CHARLESTOWN POND, RHODE ISLAND

INTRODUCTION

As part of the Salt Pond survey, there was a need to know where benthic plants grow, the kinds of plants that colonize the lagoon bottom, and why these particular plants grow better in some habitats rather than in others. The modifying influence of the presence of these benthic plant communities and their importance to the welfare of many organisms in various trophic levels in the scheme of lagoon life justified a serious study of the vegetation.

Charlestown Pond lagoon was a fortunate choice for the present study because after fifteen years of ecological study the pond is beginning to assume the classical stature of an environment with an intense and lengthening history of research. This lagoon is a good model of a semi-closed, undisturbed tidal system with certain definable characteristics which are responsible for the high bioproduction. The benthic vegetation reflects these characteristics dramatically.

METHODS

Benthic plant standing crops for Charlestown Pond were determined by sampling at stations established on a number of transects which emphasized cross sections of the total area of the estuarine system. These sampling stations (shown in Figure A-1) emphasized the natural gradients including tidal flow, salinity, bathymetry, and bottom type. These ends were accomplished by running transects along the major axes of the embayment and crossing these axes at right angles to include basins with shoreline communities as a function of bottom type and depth.

Sampling about every two weeks for 14 months was accomplished with a specially designed harpoon coring device designed by the writer. This apparatus consisted of an eight-foot-length of copper pipe fitted with a brass-fingered corecatcher and a butcher's meat saw blade which provided an excellent sawtooth edge for cutting the plant vegetation, the root systems, and the bottom sediments. The harpoon sampler was operated by casting it vigorously through the water column into the bottom, then filling the pipe with water to the top, inserting a sponge rubber ball as a valve and then forcibly removing the core from the sediment. A sluicebox was used to separate plant material from cobble, shell, and sand. The average core length recovered in fine sediments was about 40 cm. long and in coarse sediments, from 5 to 8 cm. long. The sample included blades, petioles, stems, and root systems of the attached plants. Five samples, using the harpoon tube, were obtained at each station each sampling period. An average from the five samples was then used for the sample value.

Fresh samples were washed free of sediment, returned to the laboratory, carefully washed to remove shell and animal material and separated by plant species. Plant material was then minced and placed in special pre-weighed aluminum tares. The samples were dried at 105°C. for 28 hours or constant weight. The samples in their tares were then weighed on a semimicro Mettler balance but between drying and weighing were retained in storage in a dessicator. The values were plotted in terms of space and time in frequency polygons.

Seeds of Zostera were obtained during the spring sampling periods with the harpoon sampler and estimates made of their density per M^2. Additional samples were taken at other localities to form a grid between the formal sampling stations for purposes of obtaining better dispersal information.

Spore bouyancy was determined on spores forcibly released by bringing plants into the laboratory and exposing them to higher temperature and light conditions than those in the environment. Sporulation often followed immediately, whereupon the spores were suspended in an improvised slit-cell composed of paired coverslips spaced 0.5 mm. apart and cemented on three sides, and inserted on the stage of a horizontally oriented compound microscope for observation.

Phytoplankton standing crops were measured by obtaining chlorophyll a values expressed in micrograms per liter. Although it is recognized from data unpublished by Richards and Conover that different division populations of phytoplankton, as well as the states of the population in terms of age, have a very important effect on the chlorophyll content of a plant cell, a rough estimate of the standing crop of phytoplankton can be determined for the benthic plant communities by using a modified light and dark bottle method. Large one meter wide-mouthed jugs, to serve as dark bottles, were taped with cloth electrician's tape and inspected for light leaks.

The light bottles were unmodified. The jugs were mounted in racks in the first part of the study, but later were suspended from an anchored drop line and placed at the surface and at one meter. Oxygen was measured by the Winkler method as well as by using a yellow springs oxygen meter. Production was estimated by graphic integration of the water column for phytoplankton and related to dry weight of the phytobenthon, and converted to g. C/day using the factor of 1 ml. O as equivalent to 0.53 mg. C. Phytobenthon production was estimated by subtracting the O_2 difference between light and dark bottles with phytobenthon and phytoplankton from bottles with only phytoplankton. CO_2 changes were measured by pH changes using an L & M pH meter 12 vac to 117 vac converter and battery. Eh was determined with the same pH meter using platinum electrodes.

GENETICS

Very little work has been done on the genetic constitution of marine plant populations. Those workers who are conducting studies in the ecology of benthic marine plants are in an embarrassing situation because plants in one part of the world have been described morphologically as the same species as those studied in other parts of the world, despite differences in latitude, water masses, climate, and continental barriers to circulation continuity. Genetically these widely separated plants may have entirely different physiological patterns of growth and reproduction periodicity.

This suspicion was raised for several well-known species studied in southern New England waters (Conover, 1958) and in the Gulf coast region of Texas (Conover, 1964). Without a firm knowledge of the genetic constitution of the plant communities we are dealing with, there are bound to be limitations to our analysis due to genetic differences. We must acknowledge this limitation at the outset. One can assume that the plants we are studying may include hybrids.

As a safeguard, all taxons are defined in the study as morphological entities, either on, near, or remote from particular "well-known or typed species" and described in the literature for this particular area (Taylor, 1957). The writer does imply that the results interpreted for the response of taxons in these waters does not necessarily apply to taxons which are morphologically identical but which occur in other areas such as the Gulf of Maine, the New Jersey coast, or the

Carolina Bays. The reason for this assumption is obvious. We are dealing with gene pools, some of whose taxons may range outside the ecological limits of these particular taxons. As a consequence, the physiological adjustment of plants in one part of the geographical range may be different genotypically.

In the list of species given (Table 7-1), the reader will note that there is no commentary regarding the graded identity of each taxon. These data are available in the writer's files and will be published in papers evolving from this report. It is hoped that the unknown variables can be more clearly identified in the future by employing cytological and chemical taxonomic techniques to determine any particular taxon under scrutiny.

TABLE 7-1

IMPORTANT ALGAL SPECIES IN CHARLESTOWN POND, R. I. AND THEIR SEASONAL OCCURRENCE IN THE LAGOON

Species	Seasonal Occurrence	Growth Periodicity
PHANEROGAMS		
Ruppia maritima L.	perennial	SO/AMJJA
Zostera marina L.	perennial	all year
CHLOROPHYTA		
Ulva lactuca L.	all year	all year
U. lactuca var. *lattissima* (L.) De Cand.	" "	" "
Chaetomorpha linum (Mull.) Kutz.	" "	SOND/MAMJJA
Cladophora gracilis (Griff. ex Harv.) Kutz. f. *tenuis* Farl.	" "	SOND/MAMJJA
C. rudolphiana (C. Ag.) Harv.	" "	SOND/MAMJJA
Rhizoclonium riparium (Roth) Harv.	MAMJJAS	MAMJJAS
Enteromorpha clathrata (Roth) J. Ag.	all year	all year
E. compressa (L.) Gev.	MAMJJA	MAMJJA
E. intestinalis (L.) Link	all year	all year
E. plumosa Kutz.	SOND/AMJJA	SOND/AMJJA
Codium fragile (sur) Hariot, subsp. *tormentosoides* (Van Goor) Silva	all year	all year

TABLE 7-1 (cont.)

Species	Seasonal Occurrence	Growth Periodicity
PHAEOPHYTA		
Arthrocladia villosa (Huds.) Duby	?/SOND/?	SOND/?/?
Ascophyllum nodosum f. *scorpoides* (Hornem.) Reinke	all year	ONDJFMAM
Ectocarpus confervoides (Roth) Le Jolis	SO/JFMAM	SO/JFMAM
E. siliculosus (Dillw.) Lyngb.	JFMAMJ	JFMAMJ
Petalonia fascia (Mull.) Kuntze	DJFMAM	DJFMAM
Scytosiphon lomentaria (Lyngb.) J. Ag.	NDJFMA	DJFMAM
Fucus spiralis L.	all year	ONDJFMAMJ
F. vesiculosus L. (senso lato)	" "	"
RHODOPHYTA		
Fosliella le Jolisii (Rosen.) Howe	MAMJJASO	MAMJJAS
Agardhiella tenera (J. Ag.) Schm.	all year	S/AMJJA
Gracilaria verrucosa (Huds.) Papenf.	" "	SO/?/AMJJA
Champia parvula (C. Ag.) Harv.	SO/MJJA	S/MJJA
Lomentaria baileyana (Harv.) Farl.	SON/MJJA	S/MJJA
Ceramium rubrum (Huds.) C.Ag.	MJJASO	SON/AMJJA
Spyridia filamentosa (Wufl.) Harv.	SO/AMJJA	S/MAMJJA
Chondria baileyana (Mont) Harv.	S/JJA	S/JJA
C. sedifolia Harv.	JJA	JJA
Polysiphonia harveyi var. *arietina* (Bailey) Harv.	SON/JJA	SON/JJA
P. denudata (Dillw.) Kutz.	AMJJAS	AMJJAS

BENTHIC PLANT COMPOSITION

Benthic plant communities of Charlestown Pond include some of the more ubiquitous quiet water plants of the lagoons of southern New England. The two marine, immergent phanerogams present are *Zostera marina* and *Ruppia maritima*. Together these species occupy the entire embayment of the lagoon. In addition, there are benthic marine algae which include some of the more important taxons in the plant biomass of the bottom community, including: *Gracilaria verrucosa*, *Agardhiella tenera*, and *Polysiphonia harveyi*. Some algae are epiphytes on the sea grass, Zostera, including: *Ceramium rubrum*, *Chondria baileyana*, *C. sedifolia*, and *Champia parvula*. Other red algae of less significance in the total economy of the pond are listed in Table 7-1.

In season, the following browns are found in the estuary: *Scytosiphon lomentaria*, *Punctaria latifolia*, *Ectocarpus confervoides*, *E. siliculosus* and occasionally *Desmarestia viridis*. Appearing in some restricted areas near the breachway are *Fucus vesiculosus* and *F. spiralis*. *Ascophyllum nodosum f. scorpoides* occasionally is found on the shoreline marsh fringes but there is not great development of Ascophyllum in the Charlestown-Green Hill estuary in contrast to many other southern New England estuaries. Dense communities of Ascophyllum do develop in the intertidal zone in the vicinity of rock outcrops along the Rhode Island coastal region. Ascophyllum communities are far better developed in estuaries of the Gulf of Maine and the Bay of Fundy.

Among the greens, *Cladophora rudolphiana* shares a co-dominant role in the same habitats with *Chaetomorpha linum*. A similar dominance of these species was noted by Dexter (1947) in a tidal estuary on Cape Ann, Massachusetts. Several species of Enteromorpha, including *E. clathrata*, *E. compressa*, *E. intestinalis*, and *E. prolifera*, are common. *Ulva lactuca* is present but is not in dense communities. *U. lactuca* var. *latissima* is found in some of the more brackish embayments including Fort Neck and Green Hill Pond. Other than minor species, which are listed in Table 7-1, there are a rather limited number of species of benthic plants present in the Charlestown and Green Hill Pond lagoon.

An additional list is given of the more typically open coastal species which can be found at the entrance to the breachway along the open sound, but these taxons are of little or no consequence in the estuary (see incomplete, unchecked list by Hawthorne, 1960).

More recently, two additonal algae have invaded the pond. *Codium fragile* s. sp. *tormentosoides* was not present in the estuary until the spring of 1964. Since 1963, this species has been found in almost all of the Rhode Island lagoons, estuaries, and embayments. Another species, *Arthrocladia villosa*, was observed only in a few tide pools in open coastal communities. This brown alga has now begun to appear in real abundance in Rhode Island lagoons. In Great Salt Pond estuary, six miles east of Charlestown Pond, new Point Judith, there is a considerable development of an Arthrocladia community. This particular species has attained its greatest standing crop of the year in the fall months of 1965. Very few plants of this species were found in Charlestown Pond during the survey, but at the present time this uncommon taxon is definitely on the increase along with *C. fragile* s.sp. *tormentosoides* in several coastal lagoons in Rhode Island.

The vegetation elements which represent the major biomass of benthic plants in Charlestown Pond include *Zostera marina*, *Ruppia maritima*, *Chaetomorpha linum* and *Cladophora rudolphiana*. All other plant species in the estuary are far below the standing crop of these few dominants. Each estuary along the southern New England coast, from Chatham, Massachusetts to Stafford, Connecticut, has a somewhat different species composition of benthic plants. The reasons for this are probably various.

One observation in a casual investigation of many estuaries along this coast is the presence of a greater diversity of benthic plants in those estuaries which are adjacent to rocky shores. By contrast, estuaries which are adjacent to long stretches of sandy beach have relatively few dominant species. Charlestown Pond is typical of the latter situation as it is located adjacent to a sandy barrier beach that extends many miles both in a northeasterly and southwesterly direction. The man-made rocky rip rap and the presence of many subtidal large boulders covered with benthic plants in the nearshore waters adjacent to the breachway might upset this argument. However, the stone rip rap is limited in area and currents are swift in the breachway, hence limiting these habitats to high metabolic types of plants. The boulders outside the breachway are at depths exceeding 3 meters or more which may not permit intertidal and shallow water, subtidal-adapted plants to colonize. The question remains an open one, certainly, but the pattern is very convincing wherein there is a correlation between lagoon plant population diversity and the nature of the adjacent coastal substrates and algal populations which colonize them.

HYDRODYNAMICS AND EDAPHIC RELATIONSHIPS

Since it is important for a standardization study of a non-polluted lagoon to assess the role of suitable and unsuitable habitats for benthic plants, an analysis is in order to consider the mechanical kinetics of these relationships. Charlestown Pond lagoon sediments may be classified, according to the geologist's criterion, in terms of grain size, mineral composition, and per cent carbon, as given by Dillon in Volume II (1964) under the section in Geology. However, the criterion used did not consider energy, the sediments, and the water column together in a dynamic system of interrelated events. To fully realize these integrated effects upon living communities, a study was conducted to relate bottom plant community distribution with the hydrodynamic properties of water movement, sedimentation processes and the substrate.

An examination of benthic plant attachment mechanisms (described in the systematic literature as well as in many ecological papers; see review in Fritch, 1945, and Conover, 1958, 1964) separates benthic marine plants into four categories: (1) lithophytes, requiring a hard, rocky substrate; (2) clastiphytes (new term suggested[1]), which are plants which inhabit loose sediments by some type of extensive rhizome or root development; (3) epiphytes, ranging from paraphytes to parasites which are attached to, or invade, the tissues of host plants; and lastly (4) a category which includes plants in "drift-communities" which may or may not have begun as lithophytes. In terms of plant types which occupy one or more of these substrates, it is believed that this relationship is genetically controlled. Some plants fall strictly into one of these four categories while others overlap into more than one.

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[1] Clastiphyte = a plant having rhizoids or a root system serving as an adaptation to habitats characterized by loose unsolidated sediments or clastics from sands to clays.

In Charlestown Pond, plant community separation on the basis of these four types of substrate preference is very revealing. Most of the plants in Charlestown Pond belong to the clastiphyte category. Included in this group are Zostera and Ruppia which comprise over 80 percent of the benthic plant biomass. The next most important group is the lithophyte and drift groups which commence life as lithophytes but soon join the drift community. These include species of Cladophora, Chaetomorpha, Enteromorpha, Gracilaria, and Polysiphonia, among other genera, which germinate on sand and shell particles, grow to some size and are then transported into the sea grass beds or elsewhere as part of the drift community. The epiphytes are third in importance (see Brown, Volume II, 1964).

Church (1908) described how benthic plants weighed their "anchors", e.g. lithophytes growing to full size and then weighing their "anchors" (the pebble and cobble upon which they are attached and grow). As a plant increases in size, it may ultimately buoy up and float away carrying its substratum with it. This phenomenon occurs if the substratum is small and if currents have sufficient strength to move the plant with its substratum. Conover (1958) has mentioned the importance of this type of transport mechanism which permits the development of "drift-communities" in New England and some Texas lagoons.

Where there is current-scouring or movement in Charlestown Pond, some plants are winnowed out by currents if supported on small substrates of insufficient mass to hold them in place. These plants are then moved into deeper water away from the shoreline areas where sporulation was initiated (Conover, 1958). This mechanism explains the development of "drift-communities" of some taxons in the deeper waters of Charlestown Pond where there is little or no solid non-living substrate for initial attachment.

The intertidal and subtidal apron of coarser sediments fringing the shoreline around Charlestown Pond is a very unstable, changeable habitat for benthic plants. Ice-scouring, wave transport, and tidal exposure on the beach minimize plant colonization in this zone. However, the firm, sandy apron is a site of germling establishment for many red, brown, and green algae. The importance of this subtidal apron of coarse sediments as a seeding ground is further emphasized because this zone constitutes approximately 600 M^2 of the lagoon bottom area in Charlestown Pond alone. In time, wind-waves and currents move growing plant germlings with their tiny substrates of coarse sand and shell into deeper water. Tidal exposure causes death to many of these plants on the apron. Others are destroyed by wind-wave transport onto the beaches to form mounds of dead sea wrack. Also, many plant spores are neutral to positively bouyant in normal sea water (Table 7 - 2). Consequently, more spores are moved onto the fringing shingles of the shoreline to the leeward of the prevailing wind rather than being deposited in the deeper basins. In Charlestown Pond, the pattern of distribution of small germlings is very conspicuous. Because of the mechanism just described, the plant biomass of the lagoon basins is greater by 15 to 20 per cent in Charlestown Pond than it would be in the absence of this phenomenon.

Conover's (1965) explanation for the sharp drop-off in species occupancy of habitats within higher current velocity regimes would appear to fit those examples in the lagoon where the mechanical removal of plants by tidal currents plays a prominent role. Since many current tracks (Figures A-4 and A-5) in the Charlestown Pond lagoon characteristically attain maximum velocities in excess of 20 cm. per second, with a few in excess of 50 cm. per second, transport by currents could account for the mechanical selection of some plant species which do occur in current regimes in excess of 20 cm. per second second. This is a good example of selection in the Darwinian tradition.

Undoubtedly, transport and lodgement of the germinating seeds of Zostera and Ruppia in habitats subject to tidal currents in excess of 20 cm. per second reduces the opportunity for recolonization of current-swept, denuded areas. However, the mechanism may promote the broadcast dispersal of seedlings

TABLE 7-2

BOUYANCY TEST OF THE ZOOSPORES AND AKINETES OF SOME GREEN ALGAE* IN CHARLESTOWN POND, RHODE ISLAND

Run	Species	Salinity	Movement	Bouyancy	N.
1	Cladophora rudolphiana	28 o/oo	none	82% positive	20
2	Chaetomorpha linum	28 o/oo	none	76% positive	32
3	Enteromorpha clathrata	28 o/oo	none	91% positive	19
4	Enteromorpha intestinalis	28 o/oo	rapid, confined	84% positive (bias)	41
5	Cladophora rudolphiana	15 o/oo	moderate, random	71% negative	33
6	Chaetomorpha linum	15 o/oo	none	83% negative	27
7	Enteromorpha intestinalis	15 o/oo	moderate, random	94% negative (bias)	19

*Spores liberated in laboratory under varying light and heat treatment and pressure. All experiments run at 20°C. for no longer interval than 10 minutes. See methods for details.

in the lagoon. Where plant beds are already established, continued seeding in the bed is encouraged by the protective drag against the current of the fully developed attached plants in the community. Counts of germinating seeds per M^2 support the above opinion.

In the two sea grasses, the dehiscence of the blades and fruiting stalk and the fate of the plant material is intimately associated with seed dispersal in lagoons. Examination showed that the seed pods in both sea grasses tend to be retained on the stalk until after dehiscence. Seeds retained in the pods are swept along the bottom and in windrows onto the beaches. During this period of transport of the dehisced stalks and blades, some of the seeds are apparently knocked free and fall to the bottom. Some seeds are retained in their pods and become lodged in the mat of dying and dead plant remains on the bottom of the basin. As a consaquence, one can appreciate the role of water movement, affected by wind and tide, as a major factor in the distribution and dispersal of sea grass seeds.

Dispersal of the seeds tends to fall in rather well-delineated regions of the lagoons, dependent upon the current systems (Figures A-4 and A-5) and those factors which influence them. Superimposed upon this pattern of dispersal is the degree of favorability of the environment into which the seeds are finally deposited. Seed distribution data show that the larger number of seeds found in the estuary in the month of March were distributed in the soft muds of the basin. The next most important locale was on the sandy aprons along the leeward shoreline. Those areas of least seed deposition were on the sandy shingles of the windward shoreline, on sand bars under the influence of strong tidal currents, and within the paths of current-swept channels, especially in Central Basin. Some seeds were lost from the lagoons and piled up on the beaches or transported into the black ooze-filled eddys within the small embayments around the periphery of the pond where they failed to germinate.

From Zostera seed data (Table 7 - 3) a similar pattern may be inferred for algal spores ranging from 5 to 50μ in size, under similar hydrological circumstances. Spores are moved about by currents until attachment by contact is possible. The weak forces of adhesion, due to the presence of sticky polysaccharides, assures the final lodgement of spores under normal circumstances. Under the influence of strong tidal currents, spores in current-swept habitats may be tumbled about through a turbulent water column and deposited anywhere at any depth where a firm substrate exists. In quieter waters, during calm periods when sporulation occurs, the natural bouyancy, whether positive, neutral, or negative, may dictate the zone of spore lodgement. Windrowing appears to concentrate spores along the sand shingles or aprons of leeward shorelines. Counts of algal germlings after a period of sporulation (Table 7 - 4) supports this idea.

TABLE 7-3

THE DISTRIBUTION OF ZOSTERA SEEDS, GERMINATING AND NON-GERMINATING IN CHARLESTOWN POND IN MARCH, 1963.

Location: Stn.	8C	7B	6B	WB cove gyre	WCB	4A	4B	ECB
No. seeds/M^2:	0.4	7	13	23	0.5	7	9	14
No. seeds germinating/M^2:	0.2	5	11	0	0.4	5	6	9

Legend:

Station	Description of station habitats
8C	1 meter MLW, SW windward shore, medium sand and shell.
7B	2 meters MLW, mid-pond, silty sand with organics, plant beds.
6B	1 meter MLW, NE leeward shore, medium-coarse sand, cobble, shell.
Cove gyre	0.5 meter MLW, NE shore, fine silty, clayey sand, black organic-rich ooze.
WCB	1 meter MLW, W shore, medium-coarse sand, cobble, shell.
4A	2 meters MLW, mid-pond-west, silty sand with organics, plant beds.
4B	2 meters MLW, mid-pond-east, " " " " " "
ECB	1 meter MLW, NE leeward shore, medium-coarse sand and cobble.

Note: see Figures A-1, A-6, and A-7

TABLE 7-4

THE DISTRIBUTION OF SOME ALGAL GERMLINGS (LESS THAN 3 CM. HIGH) IN VARIOUS HABITATS IN CHARLESTOWN POND, RHODE ISLAND IN MAY, 1963.

Species Stn:	8C	7B	6B	WB cove gyre	WCB	4A	4B	ECB
Agardhiella tenera	42	0	196	0	31	0	8	128
Ceramium rubrum	71	210*	114	0	41	0	3	96
Chaetomorpha linum	52	101**	76	0	27	0	11*	23
Cladophora rudolphiana	43	97**	58	0	86	0	0	14
Enteromorpha clathrata	11	0	28	0	66	0	0	21
E. intestinalis	38	0	32	0	71	0	0	89
Polysiphonia harveyi v. *arietina*	8	0	18	0	2	0	0	10
P. denudata	13	0.2	21	0	0	0	0.1	6

Note: See Figure A-1 and Table 7-3 for legend describing stations and locations. All plants on sand, pebble, or shell substrate unless stated otherwise.

* Epiphytes on Zostera.

** Epiphytes on Cladophora and Chaetomorpha.

Undoubtedly the benthic plant recruitment in a lagoon depends upon the outcome of spore dispersal patterns. Some algal spores may even be taken airborne (Duncan Blanchard, personal communication) by bubble-bursting-transport from sea to air and thence transported miles in a cloak of water vapor and dropped at some remote place. The luxurious benthic plant colonization in shallow embayments may depend partly upon the hydrodynamic and sedimentary processes which characterize the environment.

The recruitment areas for many new plant crops in Charlestown Pond are localized (1) along the shoreward or moraine side of the lagoon embayment, (2) on the jetty rip rap at the entrance to the lagoon, and (3) within the many extensive Zostera beds in Central and West Basins. The sea grass bed community is supplied with new plants not only from seed, but also from germlings of algae which overseason and reproduce spores among the stands of phanerogams. A very small fraction of the recruitment of new plants comes from scattered solitary plants growing on shell and pebble which are widely scattered on sandy bottom in areas least populated by the attached plants. These areas of minimal plant occupancy in Charlestown Pond are localized along the seaward semicircle of the embayment where hurricane and storm transport of the dune sands spills into the lagoon from the barrier beach (Dillon, Volume II, 1964).

One necessary quality of a substrate required by attached plants is firm support without burial. There is some minimum limit of supporting quality of a sediment which may be measured as the penetration of a suitable weight with respect to time (penetrometer index). In flocculent silts and clays, penetration measurements indicate high rates of rapid burial. Some benthic plants, including Zostera, grow poorly or fail to colonize in flocculent silts and clay sediments which are usually associated with estuarine "gradient zones" (Rochford, 1951; Conover, 1958). These "gradient zones" are developed where the salt-water meets the fresh-water at the steepest interface gradient. The writer has found that as long as the supporting qualities are above penetrometer rates of 2 cm./sec. benthic plants can, and do survive without serious burial.

In Charlestown Pond, there is a limited flocculent silt zone (penetrometer readings = 3.5 cm./sec.) in the upper two "kettle hole" depressions of Fort Neck embayment (Stations 1, 1a, and 2; Figures A-1 and A-7). Very few Zostera communities are able to persist in this habitat. However, Ruppia maritima communities survive. This may be due to the lower tissue density in Ruppia than in Zostera. Also, there is, in Ruppia, an extensive rhizome development which balances the stem and leaf body of the plant. Drift-community species such as Gracilaria verrucosa and Agardhiella tenera tend to be buried in flocculent silts and are poorly developed and moribund in the Fort Neck area. In some of the basins such as in West Basin, where there is a fair accumulation of soft silty sands and organic oozes, some plants are buried. However, this layer is quite thin and the supporting quality (penetrometer readings = 1.3 cm./sec.) of the basin sediments is fairly good. West Basin sediments, despite a high organic content, support a fairly rich rooted and drift vegetation.

Measurements and observations of individual plants in various sedimentary-hydrological habitats vary in terms of the actual well-being of the individual plants in the community at a given time. The healthiest and best developed plants having the most leaves, best developed root system, greenest leaves, highest cell turgor, and minimal epibiota development were observed on the more exposed sandy shingles and bars of the lagoon rathern than in the silty, sandy basins where the largest standing crops occur (Figures A-20 and A-24). Individual plants are best developed where there is coarse to moderate sandy bottom, fairly high velocity tidal currents (>18 cm./sec.), and moderately shallow water (<1 meter at MLW.). Examples of these habitats include (1) the shell and cobble-strewn bars in the path of the tidal currents which sweep out of the breachway westward to the western portion of Central Basin (Station 4 bar; Figures A-1, A-4, and A-6), (2) the sandy shingles flanking the narrows between Central and West Basin, (3) the margin of the sandy alluvial built out from the breachway entrance into Central Basin, and (4) along the sandy cobbley shore of both the southern and northern margins of Central Basin, and the northeast shore of West Basin.

The well-developed individual plants are rather widely spaced in the community instead of being closely pressed in dense communities as in parts of Central Basin (Stations 4a, 4 and 4b). In dense communities, individual plants are never as well developed and healthy. This reminds one of the isolated trees on a savanna which are much fuller, better developed trees than those growing in close stands in a dense forest.

One explanation for the enhancement of good plant growth in current-swept habitats is covered in the assimilation and diffusion studies by Conover (in this volume). He asserts that assimilation in marine phanerogams is largely through leaf, petiole, and stem organs rather than through the root system. Also, he states, the substrate probably plays a relatively minor, but not negligible role, in the supply of nutrients for the normal growth of rooted plants. He bases his assumption on the fact that most of the year the root area is only a small fraction of the leaf area. Hence, he deduces, 10 or 11 months of the year these plants derive their nutrients largely from the water column. Moreover, if the stem and leaf organs are of primary concern in assimilation, then the movement of water should be directly correlated with metabolism and growth, according to his experimental evidence.

Another consideration of benthic plant production is the observation that _Zostera marina_ and _Ruppia maritima_ apparently grow best in protected lagoons in habitats where there exist relatively strong currents (10 to more than 30 cm./sec.). Non-quantitative observation of Zostera communities in the coastal waters of southern New England by the writer suggest that the large bulk of the sea grass biomass does occur in quiet embayments and lagoons, not in open coastal waters. It is paradoxical that one finds current-adapted plants, including the sea grasses, occurring largely in protected lagoons.

One explanation is that there are two factors involved. First, there is the question of maximum depth for growth which is a function of light penetration and light quality. None of the Zostera beds occur at depths greater than 2 to 2½ meters in Charlestown Pond or any of the coastal embayments studied by the writer in New England coastal waters. Second, storm winds do not transform enough wave energy in lagoons and embayments to dislodge and uproot the attached plant communities. In the open coastal areas, heavy seas and swift currents minimize plant colonization even though all other factors may be favorable. There is an example of an open coastal sea grass, *Phyllospadix ssp.*, that is capable of withstanding considerable storm wave-action. This taxon is able to persist in open coastal waters in the Pacific Ocean in the vicinity of Palos Verdes peninsula, California. Doubtless, this is due to the well-developed rhizome-root system of these plants. By contrast, Zostera rarely develops in New England waters around headlands or other exposed coastal features where wind-wave attrition is severe.

Quantitative observation by the writer of the growth pattern of *Thalassia testudinum*, a plant with a similar growth habit to that of Zostera in Gulf and Caribbean waters, indicates that best growth of Zostera's tropical cousin occurs where there are relatively strong currents in embayments ranging from one half to one knot (25 to 50 cm./sec.). But Thalassia communities do not colonize really exposed coastal areas. The limitations to exposure by attached Thalassia plants to heavy tropical storms is cited in the examples of the widespread destruction of plant communities by hurricanes ("Donna" in 1960 and "Betsy" in 1965) in the Florida Bay section of the Everglades National Park.

Schumacher and Whitford (1965) have indicated that a current flow of 50 cm./sec. may be an upper limit for metabolic requirements of some plants. Conover (in this volume) has more data including marine plants suggesting that some upper metabolic limit related to the effect of current and turbulence does exist for some species populations in agreement with Schumacher and Whitford. The data for both studies suggests that metabolism-limiting due to the swift currents and high turbulence in some habitats may affect the growth of benthic plants before current velocities attain force enough to remove the plants mechanically. Both phenomena are probably important agents related to the local distribution of sea grasses in coastal waters.

GROWTH

Seasonal Growth of Benthic Marine Plants.

The seasonal histories and growth of the few dominant species of algae and sea grasses in Charlestown Pond are shown in Figures A-20, A-21, A-22, and A-23. These data are presented in frequency polygon projections of the standing crop measurements per M^2. Additional data for growth cycles are indicated in Table 7-1. It will be noted from these data that the plant biomass in Charlestown Pond consists of species populations which are mostly warm to cool temperate rather than boreal forms. Other important taxons (Table 7-1) include some spring and fall growth forms, but the great bulk of the minor species are warm season forms. Consequently, the spring and summer months are of greatest importance to plant growth. Since the minor taxons in the estuary are of little or no importance in terms of the plant biomass, these data are not included in this report. Of interest is the fact that there is a preponderance of warm temperate species.

The seasonal periodicity of the species populations reported here follow the same trends indicated for them in a study made by Conover (1958) in Great Pond Falmouth, Massachusetts. Moritoshi (1950) reported a somewhat different seasonal periodicity for Zostera marina in Japanese waters at somewhat lower latitudes. The emphasis for Zostera marina in his study in the vicinity of Kumi Bay on the island of Kyushu indicated that maximum growth of this species occurred in Japan from May to September and declined during winter and spring, indicating that growth took place the year round. By contrast, he states, Zostera nana, a species not present in New England waters, had a different periodicity and generally flourished best from April to June and declined in summer, fall, and winter.

It is interesting to note that Thalassia testudinum, growing in some Texas lagoons along the coast of the Gulf of Mexico, follows the same growth periodicity as Zostera nana in Japanese waters. Reproduction in Zostera marina in Charlestown Pond began with fertilization in May, seed production from May to August, seed dispersal accompanied by dehiscence of the blades in late August and early September, germination of the seeds from January through March, and the development of the new crop of small plants through the next summer. It was not clearly determined how long it takes for individual Zostera plants to attain sexual or reproductive maturity before viable seed could be produced in New England waters. Casual observations indicate that plants may require two years of growth before reproduction can occur.

Zostera grows twelve months of the year in local waters, although the growth rates are low from December through March. During the winter minimum growth period, primary production was less than 100 mg./M^2 of carbon fixed per day, in contrast to 1 to 1.5 g./M^2 of carbon fixed per day in August. The standing crop in grams dry weight per M^2 ranged from over 100 grams of plant material per M^2 or 1 kilogram or more wet weight in August, to 25 grams/M^2 in February (Figure A-20). The seasonal growth trend shows a very distinct late spring and summer maximum growth period, with greatest growth rates occurring in the month of April, May, and early June, and a period of continued but waning growth from the end of October through early March.

The ecological implications of the growth and distribution of the pattern of growth in Charlestown Pond will be considered in other sections of this paper.

Ruppia maritima, similar to Zostera, grows rapidly in the warmer months of the year (Figure A-21). However, Ruppia does not grow all year, but undergoes a period of dormancy from late October through late April. In late April and early May this taxon begins to grow very rapidly and the period of maximum growth rate occurs from May through the middle of July. In early September phytoproduction of Ruppia begins to decrease. Growth in this species falls off more sharply in brackish waters than in more saline waters with the onset of autumn.

Phytoproduction in Ruppia represents only a fraction of the plant biomass accumulated by Zostera, yet this species is fourth in importance in the estuary. Standing crop maximums, in portions of Central Basin especially, do not exceed much more than 10 grams dry weight of plant materials per M^2. Considerably higher Ruppia crop / M^2 values occur in the more brackish portions of the estuary, including Fort Neck and Green Hill Pond, but the extent of such habitats in the lagoon is very restricted. Even though the distribution of Ruppia in Charlestown Pond is confined to more brackish environments than for Zostera (Zostera, 1958, 1964), sparse communities grow in the more polyhaline habitats of West and Central Basins.

The second and third most important species in the estuary are *Cladophora rudolphiana* and *Chaetomorpha linum* (Figures A-22 and A-23). Both species attain highest standing crops exceeding 50 grams dry weight per M^2 localized largely in the West Basin area and the narrows between Central Basin and West Basin. Curiously, these species populations are less abundant in Fort Neck and Central Basin. Both species form a drift-complex community which forms heavy festoons, carpeting the bottom of the estuary. These species may be competing for space with the benthic plants, including Zostera and Ruppia, in West Basin. There is reason to believe that both *Cladophora rudolphiana* and *Chaetomorpha linum* may not grow steadily throughout the year. The reader will note in the frequency polygon for both taxons that there is a break between early December and mid-January. Although the term "lo" appears in this section of the graph, the crop is merely lowest during this period, suggesting a cessation of additive growth. The isopleths, shown in the two graphs, indicate that only a trace of these species occurred during that period. This representation is misleading. During part of December and January, complete pond station sampling was interrupted by ice conver. The isopleths should bridge the time gap. There is strong indication in these data that growth is minimal from October until May. Renewed growth in May continues through August when the maximum is attained.

There is much greater seasonal growth change in the biomass of these two species in the more brackish waters of the Fort Neck section. In Fort Neck embayment, growth is best from June through September, with a decided decrease in phytoproduction after mid-November. During the winter there is a very drastic reduction in the standing crops leaving only trace amounts.

The peculiar parallelism between *Chaetomorpha linum* and *Cladophora rudolphiana* can be seen in any sample taken where these species occur in the lagoon because their filaments are completely entangled. Being co-inhabitors and co-dominants in the same habitats with the same seasonal periodicity and life form, the crop data appear as absolute images of one another. As a consequence, the same seasonal pattern for *Chaetomorpha linum* is duplicated in *Cladophora rudolphiana*.

The other taxons which make up the rest of the benthic plant population of the estuary are of minimal significance in terms of the plant biomass. However, their growth periods, given in Table 7-1, are of importance as an indicator of the plant response to the climatic regime.

The Importance of Grazing Year-Classes and Disease.

It has been pointed out by Conover (1958) and others that large year-classes of a particular scavenger or herbivore, especially gastropods such as Bittium or Nassareous, may seriously deplete a plant species population during one particular year. No such strong year-class of herbivores producing this effect was observed during the period of the second survey from 1960 to 1964.

The toll taken by a disease inflicted by bacteria or fungi, such as the great wasting disease of the early thirties that attacked Zostera communities around the world, was not detected in any of the plant populations during the survey. However, slime molds, Ophioblis and Labryinthula, were isolated routinely by Stanley Watson (personal communication) from material supplied by the writer from southern New England waters in recent years. These parasitic organisms are present but apparently in no way affect the general health of the Zostera community. As a consequence, grazing and disease can be ruled out as catastrophic events in the pond's economy during the survey period.

Biomass Increase as a Superannual Phenomenon.

The only plausible explanation for an increase in plant growth and distribution in embayments in the last few years appears to be related to the fact that in Rhode Island coastal waters there have been minimal catastrophic storms or periods of prolonged offshore winds, severe winter freezes. Also, there has been a lack of wasting diseases for a number of years.

This trend may mean that the benthic plant biomass may continue to increase year after year in tidal lagoons until some maximum climax level in the biomass is attained. This climax level may be limited by the presence of the vegetation's own metabolite concentratons which may inhibit animal as well as plant growth, acting on one hand as an antifouling device (Conover, with Sieburth, 1964) and on the other as a growth inhibitor for all organisms.

Fortunately, the benthic vegetation of Charlestown Pond was studied over several "undisturbed" or normal years. The concepts of the growth cycles studied under these conditions enables one to gain some knowledge of the cycle of growth, reproduction, and normal maintenance of a lagoon community undisturbed by local and catastrophic events. These data may have special significance to other studies since these results may serve as a standard of comparison for lagoon studies made during periods of stress.

Temperature Kinetics and the Growth of Benthic Marine Plants

An interesting aspect of the seasonal growth patterns of benthic marine plants is the marked increase or inhibition of growth related to certain seasonal temperatures. In the seasonal growth data for the dominant benthic plants in Charlestown Pond, it was noted that events in the growth pattern were related to the 18°C., 12°C., 6°C. and 3°C. isotherms in the estuary. It is possible that this temperature response is related to thermally adjusted enzyme systems which are geared to particular temperature ranges under genetically controlled circumstances. The correspondense between growth and temperature thresholds suggests an adaptation, on a climatic scale, from the primitive algae to the more highly evolved and specialized aquatic angiosperms.

In the seasonal growth data for _Ruppia maritima_, _Zostera marina_, _Cladophora rudolphiana_, and _Chaetomorpha linum_ (Figures A-20, A-21, A-22, and A-23), there is a correlation between time, temperature and the decline in the standing crops of all four species populations. The 18°C., 12°C., 6°C., and 3°C. isotherms appear to be important kinetic thresholds related to growth inhibition in Zostera and Cladophora. The first sign of reduced growth in the estuarine populations is observed in early fall along the 12°C. isotherm (Figure A-10S/B).

Apparently at temperatures below 12°C. there is minimal or no additive growth, perhaps merely maintenance growth, in many perennial species. Physiological changes result in the cessation of additive growth as standing crop and gross production data assume negative rates. On the 6°C. isotherm the first of the winter vegetation appears. At 3°C. many more of the boreal or polar species initiate growth.

Zostera (Figure A-20), as mentioned earlier, exhibits additive growth throughout the year, even during subfreezing temperatures. In terms of biomass, this species' population tends to level off but contines some additive growth during January and February in the coldest months of the year.

Ruppia maritima (Figure A-21) has a different thermal response. There is a very distinct cessation of growth in Ruppia in the fall when the 12°C. isotherm enters the lagoon (Figure A-10S/B). Growth does not keep pace with attrition below 12°C. in this species. Below 6°C. there is no growth in Ruppia and the standing crop decreases markedly. Most plants die back to mere rudiments of rhizome and root with little or no leaf material remaining.

By November the 6°C. threshold marks the period of growth initiation of many winter species populations along the coast and in the estuary. Most of these species provide negligible biomass to the lagoon. The winter vegetation is far more important within the intertidal and subtidal regions of the open coastal waters. Data for the winter species, most of which are boreal species, characteristic of more polar climes, are not given here because of the sparceness of these plants in the estuary.

In the spring, the 6°C. isotherm, on the thermal rise, takes on significance as plant growth of some of the dominant species commences. Many of the warmer temperate plants begin growth in the lagoon at temperatures above 6°C.. Included are Cladophora, Chaetomorpha, Zostera, and Ruppia. Actually, Zostera marina begins rather rapid growth six weeks earlier than Ruppia maritima. Ruppia dies back in the winter period and remains dormant as rhizome-root rudiments. In the spring the old Ruppia plants must initiate new leaves and stem tissues before a substantial plant body develops. Although the renewal of physiological growth processes in Ruppia may start earlier (when water temperatures rise to 10°C.), the growth rate is very slow until early April.

During the period when the pond is warming from 6°C. to 12°C., rapid growth takes place in Zostera. Most rapid growth rates for Zostera occur between 12°C. and 18°C. Ruppia is also geared to the 12°C. to 18°C. thermal range for most rapid growth. Reproduction in these sea grasses occurs in May and June when the 18°C. to 22°C. isotherms dominate the lagoon. Although day length and insolation intensity may be just as important as in terrestrial plant flowering periodicity, the temperature range appears to be a constant with respect to reproduction in these two species.

The maximum water temperature, around 26° - 27°C., occurs just before Zostera marina undergoes leaf dehiscence. There has been no experimental work on the dehiscence of leaf blades in Zostera related to environmental factors to the writer's knowledge. Dehiscence in Ruppia is not so conspicuous. Ruppia leaves dehisce irregularly during the warmer months. It would appear that the thermal maximum for the year represents a period of attrition, but, in Zostera especially, the new growth of short new blades develops rapidly.

The data for late summer and fall of 1961 indicates that there may have been less growth in that year than in successive years. Compare the air temperatures from 1961 with those for 1962 and 1963 (Figure A-3). In 1961 there was generally greater variation from high to low temperatures since the means of the extremes are displaced considerably from the mean temperatures for that period. The data for the cumulative radiation patterns (Figure A-3) indicate that insolation was somewhat less in 1961 than in 1962 and 1963. Also, there was greater variability in the seasonal cloud cover in 1961. The extreme water temperatures which occurred in 1961 may have been responsible for attrition.

How extreme high temperatures may affect species populations which are thermally adapted to more moderate summer temperatures remains an open question. The fact that the older tissues and organs of both sea grasses began to diminish in growth vigor during the maximum thermal period of normal years suggests a kinetic effect upon growth. However, the growth and development of small new leaves from the rhizome were apparently unaffected by temperature extremes.

Severe winter freezing conditions apparently had no noticeable effects upon Zostera or Ruppia plants, even when solidly embedded in salt-ice for weeks at a time. Cladophora rudolphiana and Chaetomorpha linum (Figures A-22 and A-23) were growth sensitive to the 6^{o}C. to 12^{o}C. isopleth expressed as growth rate maximumx for these algae. However, there was no evidence of damage or die-back from temperature extremes. Growth of both species was linearly related to thermal kinetics.

The Role of Solar Radiation:

Solar radiation has long been recognized as the source of energy for all ecosystems commencing at the primary producer level. Seasonal growth of marine phytobenthon and phytoplankton is dependent upon radiation (see review by Holmes, 1957). However, due to the genetically-controlled adaptation of boreal or polar marine plant species compared with warm temperate to tropical species, the use of illumination by these plants is limited by thermal kinetics (see section on temperature effects). Experiments have shown that various aquatic (and terrestrial) plants are limited to certain maximum insolation levels above which the chlorophyll pigments undergo degradation resulting in lower phytoproduction under intense light. The interplay of thermal and illumination kinetics in plants is still an area of controversy and widely unresolved problems.

Marine plants at this latitude (41°N) include summer, winter, and spring-fall assemblages of plants adapted to climatic regimes northerly and southerly of the study-environment. Hence, an opportunity is given an observer to witness the interplay of light and heat on plant growth. These problems so far have not been experimentally resolved.

From the Charlestown Pond data for submarine illumination (not given in this report), no correlation between light and plant growth could be drawn. Presumably this failure is due to the high variability of the daily change in energy entering the lagoon waters all seasons of the year. Only the general trend (see Figure A-3) of rising illumination during the warmer months characteristic of the latitude and the hemisphere appear in the growth data. Nothing new in the way of an interpretation of the role of light could be added to observations already reported by Conover (1958) for this latitude regarding marine plant growth and illumination.

Doubtless a longer range study undertaken through an entire sunspot cycle might provide some meaningful correlations. That such relationships exist has been shown in data for density of seaweed growth correlated with sunspot number as a function of growth and insolation. This correlation was reported in the Annual Report for 1955 (p. 24, Figure 1) of the Scottish Institute of Seaweed Research. Undoubtedly long period studies of this nature may prove worthwhile. However, there is much experimental work than can be pursued immediately.

One may conclude that thermal kinetics related to plant growth provide a much less confusing set of problems than those regarding insolation kinetics. Further studies regarding light and plant growth in lagoon habitats are in the planning stage at this and other laboratories. What will be required is a knowledge of the effects of light of various band pass portions of the visible, IR and UV spectrum known to affect growth, reproduction, and many seasonal events in the physiology of marine plants. We must know more concerning the modifications to light quality and quantity as related to growth of specific species in macro- and micro-habitats.

Production efficiency levels for various species populations and their light quality and quantity requirements must be made known. Research along this line has moved slowly. However, my colleagues here and in other countries are turning their attention to these problems.

Turbidity and Light:

R. J. Conover (1961) considered the effect of plankton-cell abundance and its affect on shading and the subsequent reduction of light by increased cell-caused turbidity. He found no significant difference in the contribution to turbidity between surface and bottom water populations in the lagoon. He inferred from his data that high extinction values were due mainly to detritus and possibly to sampling errors in the Zostera beds. In Figure 3 (Ibid.), seasonal transparency is highest during the colder months and declines in the warmer months. This is quite usual. The writer has already explored the turbidity problem in other lagoons (Conover, 1958, 1965) and concluded that seasonal winds, which roil the bottom sediments and attrition products of dead organic material in suspension, are far more important than living planktonic bodies in the production of high turbidity in shallow lagoons. In the open sea, doubtless living plankton cells together with organic aggregates constitute the major shading factor. Charlestown Pond and especially Green Hill Pond are no exception to these findings.

INTERRELATED PHENOMENA IN
CHARLESTOWN POND, RHODE ISLAND

Introduction

Environmentally oriented scholars are particularly excited about principles concerned with the initiation, growth, survival, and death of living communities and the order of magnitude of the processes on which each intricate part of the living system depends. The following discussions touch upon principles of interaction and the magnitudes of demand, exchange, loss, and recycling of matter and energy when organized into a lagoon complex. Much of what is written here is speculation, but is based upon data acquired during this and the earlier survey by R. J. Conover (1961).

Among the stimulating problems of the past few decades considered here is the question: what comparative role do phytoplankton and phytobenthon play in the economy of coastal waters, semi-closed lagoons, and embayments?

Just what is the demand of a living lagoon community upon the non-organic constituents of a restricted embayment? An assessment of this demand is made using the considerable data at hand for the community, especially gross production values. The magnitude of this estimate shows how the amounts of inorganic constituents may exceed the net amounts of any substance present at any time. As a consequence, recycling is considered a vital process for sustained bioproduction in semi-closed marine habitats.

What effect do marine plants have upon the nutrient cycles in a lagoon? The possible role of the benthic plants is described in the following account in a different light than is ordinarily accorded this part of the marine community.

Unfinished, in terms of analysis and reflection, are those questions which deal with the rates and kinds of processes which are continually taking place in sea water outside the cell membrane of living organisms. Evidence for these processes are observed in the daily and seasonal changes in data for pH, Eh, dissolved oxygen, BOD, alkalinity, CO_2 content, and catalytic activity of the sea water environment. There are data on hand (see Figures A-9 through A-13) which reveal these changes in chemical activities at various levels related to living and non-living processes. A distinct seasonal correlation (following Tully, _et al_, 1957) between pH and dissolved oxygen is demonstrated in the Charlestown Pond data. The study of this phenomenon is still in progress and will be released at a later date. These changes hint at those external-from-living processes which are so important as side chain events which make sustained bioproduction, survival, and evolution of the marine biota possible.

The importance of phytobenthon vs. phytoplankton and epiphyton in the economy of the lagoon. Planktonic and benthic algae and the sea grasses, as the primary producers in Charlestown Pond, are recognized as the source organisms of the nutrient and food chain cycles in Charlestown Pond. Using the data for the standing crop or net production of the phytobenthon and phytoplankton for Charlestown Pond, together with data for nitrite, nitrate, and inorganic phosphate, and using total phosphorus for interpretative purposes only, an estimate can be made of the rate at which benthic and planktonic plants are involved directly in the nutrient cycle.

A question raised at the inception of this study was whether phytoplankton contribute more importantly to the biomass and nutrient budgets than do the phytobenthon. Unpublished data by Smayda and Conover strongly indicate that the phytobenthon fraction is decidedly more important. This opinion is based upon some data and the argument that limited primary production data (Table T8-1) for these two plant fractions, represented by productivity measurements using light and dark bottle experiments, and standing crops any season of the year, showed a three-fold greater biomass in favor of phytobenthon. The lack of the usual open ocean phosphorus, carbon and nitrogen ratio of sixteen to one, which most nearly simulates the proportion of these elements present in oceanic planktonic cells (Redfield, et al, 1937), is never observed in the lagoon (Table 8-2, 8-3). Values of near unity or less in lagoon waters are common.

TABLE 8-1

PRIMARY PRODUCTIVITY OF PHYTOBENTHON AND PHYTOPLANKTON IN CHARLESTOWN POND, RHODE ISLAND DURING 1963*

IN MG. CARBON PER METER SQUARE PER DAY
BASED ON 1 ML. OXYGEN EQUALS 0.53 MG. CARBON

Month:	**Feb.**	**Mar.**	**Apr.**	**May**	**July**	**Sept.**	**Nov.**
Benthic Plants:	98	207	536	816	1200	1060	110
Planktonic Plants:	39	66	137	301	432	330	28

*All measurements were made at Station 4A in Central Basin

TABLE 8-2

NITROGEN (NO_3) PHOSPHORUS (PO_4-P) RATIOS FOR ONE YEAR'S DATA FROM CHARLESTOWN POND, RHODE ISLAND FOR 1963

Summary of N:P ratios for the lagoon waters of Charlestown Pond taken from Figures A-15S/B and A-16S/B. Number = pairs of data.

Ratios:	<0.5	0.5-1.0	1-4	5-10	11-18	19-29	30-40
Number:	18	75	74	35	11	5	6

Comment: Note the majority of N:P ratios for lagoon waters fall in the range between 0.5 and 4.

TABLE 8-3

AVERAGE N:P RATIOS FOR *ZOSTERA MARINA* TISSUES BY WHEELER AND HARTWELL, 1893, FOR RHODE ISLAND WATERS.

C	H	N	P
80	10	4	1

Comment: Note the author's data show a closer correlation with Wheeler and Hartwell's ratios for Zostera, the spermatophyte which dominates the benthic plant biomass of Charlestown Pond, than they do for the N:P ratio in phytoplankton, 16:1.

These low ratios suggest a dominance of phytobenthon products in lagoons rather than those of phytoplankton. Degradation products from benthic plants including P, N, and Si fractions are released in proportion to the living cell ratios. Incubator experiments show this ratio is always very low.

The reader's attention is drawn to the frequency polygons for nitrate, inorganic phosphate, and total phosphorus and molecular oxygen in Figures A-15, A-16, A-17, and A-13. Note the presence of high values of these substances at stations in the major basins of the system, especially stations 8b, 7b, 6c, 6d, 5a, 4a, 4 bar, and 4b (Figure A-1). These stations represent the sites of the highest benthic production in the system. The phanerogam, Zostera marina, dominates these communities (Figure A-20). Strong in situ regeneration pulses (rapid rise in concentration) are indicated at these stations to the exclusion of this phenomenon at other stations. The good correlation between high in situ regeneration rates and phytobenthon production and the poor correlation between phytoplankton production and the rise in P and N recycling rates strongly supports the idea that the nutrient cycles are receiving a large fraction of turnover residues from benthic plants and a much smaller fraction from planktonic plants. These same data do show that after high concentrations of N and P are formed, phytoplankton growth is then stimulated.

A third group of plants, the epiphytes, comprise a still smaller fraction of the primary producers (Brown, 1964). If one compares Brown's epiphytic standing crop data with the seasonal standing crop for phytobenthon and phytoplankton

(Figures A-19 through A-23), the evidence suggests that the epiphytic vegetation (Brown, Volume II, 1964) growing on the phytobenthon in the month of August may be equivalent to one-third of the phytoplankton production in Charlestown Pond during the peak period of annual production. Using these data as estimates of the importance of each plant fraction, it would appear that the phytobenthon contribution is primary, the phytoplankton, secondary, and the epiphyton, tertiary.

There is the question whether phytobenthon are important in the food chain directly, in comparison with the phytoplankton which are generally assumed to be the major food item of all lower trophic levels in the sea. There is a large crustacean population, including copopods, which grazes directly upon the phytoplankton in the food chain, as reported in the earlier survey by R. J. Conover (1961) and re-enforced by considerable additional unpublished data by R. J. Conover. Phillips (in Volume II, 1964) has referred to the direct use of phytoplankton as well as zooplankton by the infauna. An estimate of the benthic and planktonic herbivore populations in the pond includes many gastropods, flagellates, ciliates, crustaceans, and polycheates, and embryonic forms of various invertebrates, as well as some herbivorous and omnivorous fishes. Several species of fishes including members of the family Clupidae, _Clupia harengus_ L., _Pomolobus mediocris_ (Mitchill), _P. pseudoharengus_ (Wilson), _Alosa sapiddissima_ (Wilson), and _Bervoortia tyrannus_ (Latr.), and other species as juveniles (Mulkana, 1964) feed upon phytoplankton in the warmer months. In the tropics, there are fish that are known to feed directly on the tropical turtle grass, Thalassia testudinum, including the black drum (Pogonias cromis L.). The parrot fish feeds directly upon reef-forming calcarious algae in tropical seas. No such direct dietary dependence upon phytobenthon has been clearly demonstrated for any of the species of fishes in New England waters. However, some species are known to include benthic plants in their diet. Among these are Archosargus probalocephalus (Walbaum), Fundulus heteroclitus L. and Tautoga onitis L. (Dr. Saul Saila, personal communication).

Neither the direct use of phytobenthon by herbivores, nor the feeding habits of the marine animals is well known. There is probably a significant amount of benthic plant material consumed by herbivores and omnivores, especially gastropods, but data are scarce. It would appear that benthic plants are probably not a primary source of food for the bulk of the herbivores and omnivores in the estuarine food chain.

The plants (of all categories) are estimated to constitute well over four-fifths of the biomass in the estuary. Assume that a large fraction of the plant biomass of all classifications enters the food chain and another large fraction does not but passes directly to the lower trophic levels and is recycled. On the basis of the total plant-standing crop, the secondary producer biomass obtains its mass and energy from only a fraction of the total food resources furnished by the primary producers. A large fraction of the phytoplankton enters directly into the food chain. The writer believes that a good deal of the phytobenthon bypasses most of the steps in the living cycle food chain but is in a sense retained in the lagoon systems as a great reservoir of organic matter.

Our model now takes shape: there are three categories of primary producers - phytobenthon, phytoplankton, and epiphyton - in the pond. The phytoplankton serves as the major food source for the food chain, whereas phytobenthon and epiphyton are secondary sources of direct food, but more importantly provide organic reservoirs which support the living system in the lagoon. As a consequence, there is a constant build-up of organic matter, largely of phytobenthon, in the lagoon. The seasonal release of metabolites, including pro- and antibiotics (Conover, with Sieburth, 1964; unpublished data, 1965) and stimulating hormones from the phytobenthon reservoir, provides a fairly constant nutrient and hormonal reserve. The effect of these reserves is to provide and maintain a relatively constant high production level of phytoplankton and in turn to sustain a high secondary production of all other trophic level organisms in the lagoon.

In this model, the presence of a luxurious phytobenthon community may help to explain the enrichment of an estuarine community such as Charlestown Pond. If the phytobenthon and epiphyton do provide a more or less continuous flow of nutrients seasonally as a kind of "organic flywheel", then the rates of organic turnover in lagoons similar to Charlestown Pond may owe their sustained production to the presence of phytobenthon and epiphyton. The consequences of the phytobenthon turnover doubtless is most intense in semi-closed lagoons and embayments and less apparent in open embayments, sounds, and open coastal waters.

The Effect of Benthic Marine Plants upon Nutrient Cycles:

The usual orientation of studies related to seasonal growth of marine communities considers the effect of the environment upon the community and various species populations. The effect of a particular group of organisms upon the environment and the economy of the marine community is of particular interest if the effect is of any magnitude. The following account places an unusual emphasis on the role of benthic plants in semi-closed coastal embayments. The key question has been, why do lagoons, at any latitude, which support an extensive and luxurious growth of bottom plants, invariably exhibit impressive production levels of marine biota? If bottom plants were directly in the food cycle as the major source of food, there would be no problem. But food chains are generally related to the seasonal abundance of unicellular rather than the large multicellular plants.

In Central and West Basins of Charlestown Pond, the phytoplankton communities are generally sustained the year around at fairly high production levels according to the standing crop data (Figure A-19S/B). Exceptions to this are the poorly growing phytoplankton populations which are found only seasonally in the influx of tidal water coming in from open coastal waters. There is also a considerable fluctuation in the phytoplankton abundance in Fort Neck embayment. The growth of these unicellular plants may be dependent upon the fluctuations in macronutrients supplied by the two brooks entering the embayment (Figures A-14 through A-17, Section A). R. J. Conover (1961) gives a similar picture for the phytoplankton fluctuations in Green Hill Pond. These exceptions represent less than 15% of the Charlestown Pond area. Green Hill Pond is noted for its generally low production capacity (Conover, 1961).

How does one account for the sustained high bioproduction in Central and West Basins, especially of the phytoplankton? The reader should turn his attention to the nutrient cycles described in Section 3-1 *et seq*. (Figures A-14S/B through A-17S/B). It is obvious that the recycling rates computed indicate that there is never any seriously low concentrations of orthophosphate or nitrate in Central and West Basins, even during the warmest months of the year. If a dynamic formula for computing nutrient availability had not been used, the last statement of course would be invalid. A lack of correlation between the "static" nutrient levels, at times unmeasurable in West and Central Basins in mid-summer (due to rapid recycling), supports the argument and helps solve one of the mysteries of phytoproduction in coastal embayments during periods of so-called low nutrient availability. How do we explain this paradox?

First of all, the benthic or attached plant communities show only continued vigorous growth throughout the spring, early and mid-summer period, attaining a maximum growth during the solar thermal peak in August. No nutrient deficiency was indicated in the seasonal growth of these plants (Figures A-20 through A-24). Not only is the cycling rate of the nutrients turning over rapid enough to meet the demands, but also the benthic plants are capable of storing nutrient salts in their tissues (Conover, 1958, and others). Due to this reservoir action and the high turnover rate, there is a fairly constant supply of nitrate and phosphate as well as other required substances, including vitamins and hormones, which is available to the phytoplankton communities.

The hypothesis that nutrients are stored in the tissues of sea grasses and are subsequently released is supported by the fact that orthophosphate was always 0.5 g. at./L. higher in dense grass beds any season of the year than in the open water. Note in Figures A-16B and A-17B that phosphorous was generally higher in the bottom water, particularly at stations 7b, 4a, 4 and 4b, the sites of extensive Zostera beds.

There is another source of nutrients indirectly related to benthic plants. Remember the small eddies or gyres along the indentures of the lagoon coastline where accumulations of organic matter are concentrated (Figures A-4 and A-8)? These small organic ooze-filled eddies have large accumulations of organic matter which serve as reservoirs of decaying organic debris largely of benthic plant origin. These eddies appear to provide a constant inflow of nutrients into the estuarine system for all plants, benthic and planktonic. A simple experiment whereby measurements of inorganic phosphate were made at close spaced intervals (Table 8-4) from the center of an eddy outward into a large basin area (station 4a in Central Basin), suggests that a nutrient supply is emanating constantly from these eddy deposits, as well as the salt marshes.

It is suggested from the diffusion patterns shown in these data that a secondary source of nutrients adds to that of plant tissue storage to help provide the sustaining levels for phytoplankton growth. As a consequence, nutrient limiting is probably minimal because of the presence of large populations of benthic plants which serve as an organic reservoir for organic and ultimately inorganic residues of the required substances for plant growth.

Comparing the Production Based on Carbon:

Using the gross primary productivity data for phytobenthon and phytoplankton and using Wheeler and Hartwell's (1893) composition data for *Zostera marina* and Riley's (1941) data for the composition for the average phytoplankton, monthly and annual phosphorus, nitrogen, hydrogen, and carbon budgets for gross and net production can be drawn up for three embayments of Charlestown Pond (Table 8-5, 8-6, 8-7, and 8-8). Carbon data for the zooplankton are shown in Table 8-9. The data for epiphyton are available (Brown, Volume II, 1964) and will be given in the published results. However, the epiphyton

TABLE 8-4

CHANGES IN CONCENTRATIONS OF INORGANIC PHOSPHATE (PO_4-P) WITH DISTANCE FROM TWO EDDY-DEPOSITS OR SHORELINE MICRO-EMBAYMENT GYRES, WEST BASIN, CHARLESTOWN POND.

Distance into lagoon from gyre	PO_4-P in g.at.P/L.	Remarks
	GYRE # 1. NE of Stn. 5B**	
Center of gyre	2.83	*Sample depth, 8-10 cm. off of the bottom.
Edge of gyre	2.01	
2 meters south	1.64	Note significant change outside of gyre.
5 meters south	1.72	
10 meters south	0.81	Note values of lagoon water phoshpate
20 meters south	0.62	
	GYRE # 2. S of Stn. 6D**	
Center of gyre	2.10	*Sample depth, 8-10 cm. off of the bottom.
Edge of gyre	2.32	
2 meters north	1.88	
5 meters north	1.23	
10 meters north	0.66	Note two different gyres exhibited this same feature.
20 meters north	0.41	

Note: similar data are on hand, though much less dramatic, for the diffusion of phosphate from the salt marshes which are fairly extensive surrounding much of Charlestown Pond. This source was not discussed in the text but may be next in importance to the gyres.

*The depth of sampling in all cases was 8-10 cm. off of the bottom. No creeks or springs were observed in the area chosen for this study.

**See Figures A-1 and A-4 for location of gyres.

TABLE 8-5

ESTIMATES OF THE MONTHLY AND ANNUAL DEMAND FOR P, N, H, AND C IN CENTRAL BASIN, CHARLESTOWN POND, RHODE ISLAND, BASED UPON GROSS PRODUCTION DATA FOR PHYTOBENTHON, 1962-63, PER METER SQUARE

	Phytobenthon Gross Production Demand			
Element in gram atoms (for *Zostera marina*):	P (1)	N (4)	H (10)	C (80)
January	.036	.060	.360	3.100
February	.036	.060	.360	3.100
March	.072	.300	.720	6.000
April	.090	.750	1.800	15.000
May	.318	1.200	2.880	24.000
June	.360	1.500	3.600	30.000
July	.432	1.800	4.320	36.000
August	.390	1.650	3.660	33.000
September	.360	1.500	3.600	30.000
October	.072	.300	.720	6.000
November	.036	.060	.360	3.100
December	.036	.060	.360	3.100
Annual Total per M^2	2.38 gms. PHOSPHORUS	9.24 gms. NITROGEN	19.08 gms. HYDROGEN	159.40 gms. CARBON

TABLE 8-6

ESTIMATES OF THE MONTHLY AND ANNUAL DEMAND FOR P, N, H, AND C IN CENTRAL BASIN, CHARLESTOWN POND, RHODE ISLAND, BASED UPON GROSS PRODUCTION DATA FOR PHYTOPLANKTON, 1962-63, PER METER SQUARE PER TOTAL DEPTH

	Phytoplankton Gross Production Demand			
Element in gram atoms (for average diatom):	P (1)	N (16)	H (14)	C (106)
January	.0055	.083	.075	.540
February	.0130	.187	.164	1.170
March	.0198	.317	.278	1.980
April	.0412	.658	.575	4.120
May	.0901	1.450	1.270	9.010
June	.1080	1.750	1.510	10.800
July	.1290	2.400	1.820	12.900
August	.1175	1.870	1.680	11.700
September	.0990	1.580	1.390	9.900
October	.1223	.360	.315	2.750
November	.0084	.133	.118	.840
December	.0055	.083	.075	.540
Annual Total /M^2/total depth	0.659 gms. PHOSPHORUS	10.871 gms. NITROGEN	9.270 gms. HYDROGEN	66.250 gms. CARBON

TABLE 8-7

ESTIMATES OF THE MONTHLY AND ANNUAL STANDING CROP* CARBON CONTENT OF THE PHYTOBENTHON FOR THE THREE EMBAYMENTS OF CHARLESTOWN POND, RHODE ISLAND, 1962-63, PER METER SQUARE

Based on C content of Zostera marina	West Basin	Central Basin	Fort Neck	Total
January	9.25	14.50	6.50	36.25
February	17.75	21.00	7.00	43.25
March	22.75	22.50	7.75	53.00
April	29.50	33.00	11.00	74.50
May	38.00	44.00	50.00	122.00
June	68.00	54.00	67.00	190.50
July	111.00	80.00	51.75	257.50
August	116.00	80.00	66.50	212.50
September	63.50	54.00	41.50	140.00
October	41.00	44.00	22.50	76.50
November	21.50	28.00	9.50	56.50
December	15.25	14.50	6.50	36.25
Cumulative Annual Totals	574.00 gms. CARBON	489.50 gms. CARBON	347.50 gms. CARBON	1,298.75 gms. CARBON

*Note these values are cumulative for a perennial plant biomass.

8-11e

TABLE 8-8

ESTIMATES OF THE MONTHLY AND ANNUAL NET (STANDING CROP) OF CARBON PRESENT IN THE PHYTOPLANKTON POPULATIONS OF CHARLESTOWN POND, RHODE ISLAND, 1962-63, PER M^2 PER TOTAL DEPTH OF THE WATER COLUMN IN MG. C/L. FOR EACH EMBAYMENT*

Mar.	Apr.	May	June	July	August	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Annual Total
FORT NECK												
Chlorophyll *a*												
6.4	8.0	3.3	2.7	5.7	2.2	9.9	10.3	1.83	2.25	2.53	4.45	159.1
Carbon Content												
23.7	29.6	12.2	9.9	21.0	8.1	31.7	33.0	5.8	7.2	8.1	14.3	204.6
WEST BASIN												
Chlorophyll *a*												
3.4	1.25	.94	3.0	.91	3.9	4.2	2.8	1.83	4.4	8.8	3.8	47.6
Carbon Content												
10.9	4.0	3.0	9.6	2.0	12.4	13.4	8.9	5.9	14.1	28.2	12.2	124.6
CENTRAL BASIN												
Chlorophyll *a*												
3.7	-	1.47	1.32	0.56	0.89	7.0	2.13	1.28	2.4	1.05	-	21.80
Carbon Content												
11.8	-	4.7	4.2	1.79	2.84	22.4	6.8	4.1	7.7	3.35	-	69.68

*Based on a formula by Ryther and Yentsch (1957) for converting chlorophyll *a* to carbon (1:2:3).

8-11f

TABLE 8-9

ESTIMATE OF THE MONTHLY AND ANNUAL CARBON* CONTENT OF ZOOPLANKTON POPULATIONS IN CHARLESTOWN POND, R. I., IN 1955-57.

(Unpublished data, R. J. Conover)

ONLY SURFACE SAMPLES WERE TAKEN. FOR TOTAL DEPTH, VALUES MAY DOUBLE IN DAYLIGHT.

	M	A	M	J	J	A	S	O	N	D	J	F	Annual Totals
						WEST BASIN							
Dry wt gms./M^3	11.7	65.0	5.84	400.	368.	365.	15.3	9.26	1.66	-	0.327	26.7	486.4
Carbon in gms./M^3	2.34	13.0	1.17	80.	71.6	73.	3.06	1.85	0.332	-	0.0654	4.54	250.1
						CENTRAL BASIN							
Dry wt gms./M^3	93.5	7.70	5.84	68.4	172.	33.8	10.7	142.	5.42	105	8.46	30.5	393.9
Carbon in gms./M^3	18.7	1.54	1.17	13.7	34.4	6.76	2.14	28.4	1.08	21.	1.69	6.1	136.3

FORT NECK EMBAYMENT

NO DATA

*Carbon content of copepods (dominant organism) 25% by wt., after Vinogradov, 1953.

represents only a small fraction of the total plant production. The exclusion of these data from the budget given here is a minor loss. However, paraphyton in some waters may amount to a significant bulk of the plant population.

It is evident from these data that almost 3 grams of phosphorus per M^2 (including the entire depth of the water column) are utilized per year in Central and West Basin and about 2 grams of phosphorus in Fort Neck Embayment. As the tissues of the phytobenthon represent a cumulative growth of several seasons, the stored residual of organic matter in these plants, as indicated in Table 8-7, dramatically illustrates that there is always three or four times the amount of phosphorus, nitrogen, carbon, and other cell constituents present in the living tissues of the phytobenthon over that required for metabolism and growth requirements of the total plant community.

With data on hand given in this report, it is possible to determine how much organic matter turns over per year in "normal" years in the estuary if the data are prorated to the habitats and bottom area of the lagoon. The total amount of degradation matter derived from dead plant and animal debris is estimated on the basis of plant wrack and organic debris on the bottom and shores of the three embayments (Table 8-10). These figures are probably the least reliable of all those given. The difficulty in assessing degradation of organic matter is the immediate loss by oxidation of dying and dead organisms shortly after death and the loss of much of the organic substrate by microbial activity. If all of the

TABLE 8-10

ESTIMATE OF THE CARBON, NITROGEN, AND PHOSPHORUS CONTENT IN THE WEED WRACK OF *ZOSTERA MARINA* ACCUMULATED IN THREE BASINS OF THE LAGOON AT THE END OF AUGUST, 1964, IN CHARLESTOWN POND, RHODE ISLAND PER M^2.

Locality	Dry Wt/M^2	(80) Carbon	(4) Nitrogen	(1) Phosphorus	M^2 Basin Area
West Basin	0.60 gm.	0.30 gm.	0.0140 gm.	0.0037 gm.	2,904,768
Central Basin and Narrows	0.85 gm.	0.425 gm.	0.0212 gm.	0.0053 gm.	1,626,660
Fort Neck Embayment	0.12 gm.	0.060 gm.	0.0035 gm.	0.00075 gm.	588,950
					10,210,378

degradation products could be accounted for, one would expect this fraction to equal the amount of organic matter produced in the long term picture. One would expect a large fraction of these products to be recycled into the living system. Also, some fraction is permanently lost from the living system in the sediments, by transport to the sea, into the atmosphere, and by oxidation processes (see Section 4).

The most outstanding feature of this crudely determined cycle of turnover in a living system, given in the above account, is the prominence heretofore not given the phytobenthon as having an important ameliorating influence upon the bioproduction of coastal lagoons.

The data in Table 8-11 summarizes the total amount of carbon accumulated per M^2 in each of the three basins of Charlestown Pond. If the carbon in each basin was prorated as to habitat and took into account the differences in area, more carbon would accumulate in West and Central Basins. However, the large amount of carbon per M^2 (including the total depth of the water column) in Fort Neck Embayment clearly indicates the nature of this specialized habitat for periodic plankton blooms and the large accumulation of organic carbon in the embayment sediments.

Data for zoobenthon and zoo-nekton are missing (see Section 1), hence only the magnitude of the production cycle as inferred from the carbon data is indicated here. These estimates may serve as an index for this particular type of terminal phase lagoon which has reached a type of biological and physical climax in the cool temperate climate of southern New England.

8-14

TABLE 8-11

COMPARISON OF ESTIMATED CARBON ANNUAL TOTALS
IN CHARLESTOWN POND, R. I. PER M^2
(PER TOTAL DEPTH OF THE WATER COLUMN)

	Carbon in gms.	Percentage
West Basin		
Phytoplankton	124.6	13.0
Phytobenthon	574.0	60.0
Zooplankton	250.6	26.0
Organic Detritus	0.30	0.03
Totals	949.5	99.0
Central Basin		
Phytoplankton	69.5	10.0
Phytobenthon	489.5	70.0
Zooplankton	136.3	19.5
Organic Detritus	0.425	0.06
Totals	695.7	99.5
Fort Neck Embayment		
Phytoplankton	204.6	31.0
Phytobenthon	347.5	53.0
Zooplankton (no data)	>100. (?)	@15.5
Organic Detritus	0.12	0.018
Totals	652.2 (?)	99.6

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